

Logan River whirling disease study: factors affecting trout population dynamics, abundance, and distribution in the Logan River, Utah

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PREFACE

This report consists of five separate chapters. Chapter 1 contains results from the monitoring and evaluation of eight index sites on the Logan River and tributaries that have been surveyed since 2001. Chapter 2 encompasses research conducted by Erin VanDyke as part of an undergraduate research experience. Chapter 3 is a manuscript that was submitted to the *Canadian Journal of Fisheries and Aquatic Sciences* as part of Pete McHugh's PhD dissertation research. Chapter 4 is a continuation of Pete McHugh's dissertation research; this chapter will soon be submitted as a manuscript to a peer-reviewed journal. Chapter 5 is a synthesis of the research conducted to date on the Logan River and cutthroat trout population dynamics in the basin.

EXECUTIVE SUMMARY

The overall goals of this study are to monitor and evaluate the population dynamics, abundance, and distribution of trout in the Logan River, and to determine the present and potential impacts of disease, habitat, and interspecific interactions on the present and future status of native Bonneville cutthroat trout (*Oncorhynchus clarki utah*). Toward that goal, we have been monitoring the fish community of the Logan River at eight long-term index sites since 2001. We collect information on trout distribution, population abundance, condition, health and disease, as well as measuring key abiotic variables at each site (Chapter 1). We consider the effects of interactions between native cutthroat trout and exotic brown trout (*Salmo trutta*) with both field observations of feeding relations (Chapter 2) and in large-scale species interaction experiments. In 2003, (Chapter 3), we completed enclosure (20 m²) experiments at six sites arranged along the longitudinal gradient of the Logan River, and reared cutthroat trout in treatments with (sympatric) and without (allopatric) brown trout. In 2004 (Chapter 4), we scaled up and repeated similar species interaction experiments in 500-m reaches in three nearby tributary streams. We summarize all this information in an evaluation of the potentially synergistic effects of abiotic variables (e.g., temperature), competition with brown trout, and disease (e.g., *Myxobolus cerebralis*) on the status and trend of native cutthroat trout using some simple, population modeling (Chapter 5).

Depletion-based abundance estimates indicated that in 2004, cutthroat trout abundance decreased from the previous year at four of the six sites where they occur with small increases at the other two sites (Chapter 1). Brown trout abundance was generally similar to the previous year at four of the seven sites where they occur, with declines in abundance observed at three of the sites. For the first time since 2001, in 2004, we detected a significant downward trend in cutthroat trout abundance at four of the cutthroat trout sites. Prevalence of *M. cerebralis* in adult cutthroat trout is now at 100% at three of the five sites (2 sites were not tested in 2004); prevalence is consistently lower in the tributaries. Prevalence of *M. cerebralis* in brown trout continues to be about 15% less than that observed in cutthroat trout, and Right Hand Fork, a brown trout only site, still tests negative for *M. cerebralis* (the only site that tests negative in the drainage). We continue to see very few fish with clinical signs of whirling disease, but note that this may be because we are handling only survivors. Despite declining abundance at some sites, cutthroat trout and brown trout are generally in relatively good condition ($K \sim 1$) and demonstrate high growth and survival rates. The Logan River has been experiencing drought conditions since 2000; mean annual run-off has been less than the long-term mean. Consequently average summer temperatures are warm and discharge is low. We suspect that the

drought is having some negative influence on trout abundance; however, 2004 was the wettest year since our monitoring began in 2001.

In the Logan River we have observed several different patterns which suggest that native cutthroat trout are competing with exotic brown trout. First, these trout species demonstrate a distinct pattern of allopatry with high abundance of cutthroat trout at high elevation, high abundance of brown trout at low elevation, and only a small zone of overlap at mid-elevation, where abundance of both species is low. To better understand these interactions, in 2004, we completed an assessment of the feeding relations between the two species with consideration of ontogenetic differences in diet (Chapter 2). Diet analyses and isotopic signatures were completed on a subsample of fish from a high elevation cutthroat trout only site (Franklin Basin), a mid-elevation mainstem site where both species co-occur (Twin Bridges), and a low elevation brown trout site (Third Dam). This evaluation demonstrated several important patterns: 1) when cutthroat trout occur alone, diets of juveniles and adults were similar (90% overlap), 2) when cutthroat trout co-occur with brown trout, diet overlap between adults and juveniles is low, and 3) diet overlap between adult and juvenile brown trout is similar in allopatry and sympatry. We also observed an increase in niche width when cutthroat trout occur with brown trout as compared to when they occur alone. These results suggest the potential for competition between the two species. If, as we observed, adult cutthroat trout are forced to expand the breadth of their diet when in the presence of brown trout, and if these other, additional diet items are less energetically profitable, this shift could result in a reduction of growth and ultimately fitness of cutthroat trout. The fact that juvenile cutthroat trout do not demonstrate this increase in diet breadth when in the presence of brown trout could indicate they do not yet have the plasticity to expand their diet; if this were true, it could mean that juvenile cutthroat trout are at an even greater disadvantage, as compared to adults, when in the presence of brown trout.

Also in response to observed patterns of allopatric distribution, we completed two sets of experiments in 2003 and 2004. In 2003, we reared cutthroat trout and brown trout along the longitudinal gradient of the Logan River to determine whether competition explains the observed pattern of altitudinal species zonation and to test for temperature mediated competition (Chapter 3). In these experiments, brown trout had a negative effect on cutthroat trout growth and condition. We did not observe evidence for temperature mediated competition, as brown trout negatively affected cutthroat trout at all temperatures, and were unaffected by cutthroat trout at all temperatures. There are several experimental reasons that could, however, have masked a temperature effect. In 2004, we scaled up and completed similar competition experiments in a more natural setting, where we could look at effects at both the individual and population level (Chapter 4). Cutthroat trout were reared

alone and in the presence of brown trout in 500-m reaches of three nearby tributaries of the Blacksmith Fork River. Across all three sites, cutthroat trout growth in allopatric treatments (e.g., alone) was more than double that observed when cutthroat trout were sympatric with brown trout. Further, although differences were smaller, survival of cutthroat trout was also lower in sympatric treatments with brown trout, as compared to treatments where cutthroat trout were alone, and brown trout also appeared to suppress movement rates of cutthroat trout, (although it is important to note that movement rates were low overall). These field-based evaluations of species interactions will be complemented in 2005, with laboratory experiments aimed at gaining a better understanding of the behavioral mechanisms responsible for the competition effects observed in the field.

Finally, we synthesize our monitoring and evaluation and experimentation within a population modeling framework (Chapter 5). We first estimated trends in population growth rates at each site, and we then use these observed trends to calibrate a simple matrix model to three of the sites (Franklin Basin, Twin Bridges, and Third Dam), which adequately represent the range of characteristics observed across all eight long-term index sites. We use our own empirical estimates of age, size, survival, and growth, and the effects of competition in combination with literature-derived values of fecundity and early survival (egg-to-fry). We then used the model to evaluate the future status and trend of the site-specific subpopulations under scenarios of increased temperature, increased prevalence of whirling disease, the arrival (invasion) or removal of brown trout and associated effects of competition, and combinations of all factors modeled simultaneously. Model results indicate that while the effects of increased temperature alone are substantial, competition is highly influential. More importantly, the combination of increased temperature and competition (negative or positive effects), in the face of increasing prevalence of whirling disease, has the greatest and most consistent effect across modeled sites in determining future trend and status of this population. In Chapter 5 we also discuss the different sources of evidence which point to the importance of the tributaries as refuges. It appears that juvenile or subadult fish may rear in these less-infected tributary areas until they have grown to a body size where the risk of mortality due to *M. cerebralis* infection (or infection in combination with another factor) is low, before moving out into more dangerous mainstem areas. Like the effects of competition and disease described above, the effects of stream degradation and whirling disease may also be synergistic. In combination these results thus emphasize the importance of protecting and restoring habitat in tributary spawning and rearing areas, such that factors which appear to increase *M. cerebralis* prevalence, (e.g., warmer temperatures) via the several different pathways associated with the complex life history of the parasite, are minimized.

CHAPTER 1:
Monitoring and evaluation of factors affecting
trout abundance in the Logan River, Utah

INTRODUCTION

The Logan River, once considered one of the best trout streams in the region, still supports a popular fishery for stocked rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and the native Bonneville cutthroat trout (*O. clarki utah*). The decline in the population of the native Bonneville cutthroat trout throughout the intermountain west is evident, and only a few populations remain (Behnke 1992). However, the Bonneville cutthroat trout (hereafter referred to as cutthroat trout) in the Logan River might be one of the strongest and largest metapopulations within their historic range (Thompson et al. 2000). Many of the remaining cutthroat trout populations persist solely within headwater streams. Presently, the subspecies is recognized as an imperiled species by the American Fisheries Society (Williams et al. 1989) and is protected in Utah under an interagency Conservation Agreement; one of the primary goals of this conservation agreement is to better understand the role of introduced species in the decline and recovery of cutthroat trout - the focus of the research described herein. Brown trout were introduced into Bonneville Basin streams in the late 1800s and are presently one of the most abundant trout species in the region. Simultaneously, cutthroat trout have disappeared from much (65%; USFWS 2001; UDWR 2005) of their historic range, presumably due to the combined effects of habitat degradation and introduced species. In addition, there is no evidence within this watershed that nonnative trout have expanded their populations within the past decades. Understanding the population status and trend, the performance and condition of the trout population, habitat quality, and the current and potential future effects of disease in the Logan River is critical for the effective management of this system (Lentsch et al. 1997).

Dynamics of fish populations are directly linked to the environmental characteristics of their habitat. Physical, chemical, and biological characteristics of the environment affect growth, survival, and birth rates. Further, salmonids use different habitats at different life stages and during different seasons (Bradford and Higgins 2001; Bonneau and Scarnechia 1998; Maki-Petays et al. 1997); therefore, it is necessary to expand habitat-population relationships to larger scales that encompass the various habitats used. Physical characteristics of habitat similarly affect the community

structure and distribution of macroinvertebrate fauna and other biota. Hydrological and sedimentary networks within a drainage can explain, at least partially, the community organization of macroinvertebrate communities (Rice et al. 2001).

In addition to environmental variables, parasites and disease play an important role in determining fish population dynamics. The severity, prevalence, and impact of a given disease also depend on the interactions of several variables of the host, the pathogen, and environment (Reno 1998). Pathogens demand energy that the host would otherwise use for growth, survival, and reproduction (Minchella and Scott 1991). The occurrence of disease depends on the genetic characteristics, immunological, and nutritional conditions of the host, among other variables (Moffit et al. 1998). Diseases occur both in wild and cultured fish populations; however, while the effects of many diseases are known in cultured fish, less information is available for wild populations.

Myxobolus cerebralis, the parasitic causative agent of whirling disease, has caused severe population-level declines in some states such as Colorado and Montana (Nehring and Walker 1996; Vincent 1996; Baldwin et al. 1998); however, fish populations from other areas where fish have tested positive for whirling disease in other states (e.g., California) have not been significantly impacted. Fish samples for the Logan River have tested positive for whirling disease, but up to this point, there has been no evidence of population declines in this drainage (Thompson et al. 2000; Budy et al. 2002, 2003, 2004).

To evaluate population changes and the potential effects of whirling disease, we initiated (2001) a long-term monitoring program of the fish community at eight sites, from the upper headwaters of the Logan River (Franklin Basin) to the lower Logan River (Logan River golf course area; Figure 1.1; Table 1.1). Survey locations were chosen to maximize information on trout distribution and capture the range of physical habitat characteristics observed in the Logan River drainage. Most selected sites were previously sampled by the Utah Division of Wildlife Resources (UDWR; see Thompson et al. 2000). This allowed us to compare and contrast our results to data from previous surveys. In addition, we considered different physical (e.g., flow, temperature, substrate), chemical (e.g., concentrations of phosphorous and nitrogen), and biological (e.g., productivity) factors associated with fish abundance and distribution, as well as the presence and prevalence of *M. cerebralis* along the stream.

The overall objectives of this study are to monitor and evaluate the population dynamics, abundance, and distribution of trout in the Logan River, and to determine

the present and potential impacts of disease, habitat, and interspecific interactions on native Bonneville cutthroat trout.

Table 1.1. Elevation and relative location of eight long-term index sites on the Logan River.

| River km | Elevation | |
|----------|-----------|-------------------------|
| | (m) | Description |
| 0.0 | 2291 | Idaho border |
| 9.2 | 2023 | Franklin Basin |
| 13.2 | 1923 | Red Banks |
| 16.2 | 1855 | Forestry Camp |
| 22.5 | 1745 | Temple Fork (mouth) |
| 26.6 | 1691 | Twin Bridges |
| 36.1 | 1588 | Right Hand Fork (mouth) |
| 43.0 | 1509 | Third Dam |
| 56.8 | 1352 | Lower Logan |

STUDY SITE

The headwaters of the Logan River are located in the southeastern corner of Franklin County, Idaho (Figure 1.1). The river runs southwest entering the state of Utah in the northeast corner of Cache County at an approximate elevation of 2600 m. The two largest tributaries are the Franklin Basin branch and the Beaver Creek branch, the first one being the largest; they join approximately 2 km south of Beaver Mountain, about 10 km south of the Idaho state line. The river then runs through Logan Canyon for 64 km to reach the city of Logan, dropping to an elevation of approximately 1370 m at the eastern city limits (Thoreson 1949).

The gradient on the main stream varies from 7 - 32 m per km, and the higher gradient of the tributaries reach 75 m per km in Spawn Creek, making them predominantly white-water streams. Riffles and swift channels are common while pools are sparse. Boulders and rubble are common in the stream bottom of higher gradient sections; gravel beds and sand occur in areas of lower gradient or not exposed to the stream current, solid bedrock is also common. Impoundments are heavily silted as a result of natural erosion. The average discharge, based on a yearly average, is approximately 2.6 cubic feet per second ($0.07 \text{ m}^3/\text{sec}$).

Predominant game fish include endemic Bonneville cutthroat trout, brown trout, stocked rainbow trout (including albino strains), brook trout, and mountain whitefish. Non-game fish include carp (*Cyprinus carpio*), mountain sucker (*Catostomus platyrhynchus*), and mottled sculpin (*Cottus bairdi*).

METHODS

Field sampling

Fish collections

Fish were collected during base flow conditions using a three-pass depletion technique. Block nets were placed at the lower and upper end of each stream section (100 m sections in the headwaters and tributaries, 200 m in the mainstem). The settings on the electrofishing equipment varied depending on the stream conductivity. Effort was recorded as the time spent fishing per fixed distance, as suggested by Reynolds (1996). For smaller streams, a backpack-mounted electrofishing unit was used. For the larger mainstream surveys, a canoe-mounted electrofishing unit was used. Captured fish were anesthetized with a dose of MS-222. Lengths (mm total length, TL) and weights (g) were recorded for all fish, and in addition, fish were checked for external signs of whirling disease (e.g., black tail, deformities of the jaw or spine). When possible, 20 subadults and 10 adults from each species were kept. We classified subadult cutthroat trout as fish < 150 mm TL and subadult brown trout as fish < 180 mm TL. These fish were euthanized using a lethal dose of MS-222 and placed on ice in labeled bags after lengths and weights were measured. These fish were used for diet, health condition assessment, PCR testing for *M. cerebralis*, and stable isotope analyses, and scales were taken for ageing analysis.

Condition analysis

Length-weight relationships (by species, all years combined; Appendix Figure 1) and condition factor (Fulton's $K = [W / L^3] \times 100,000$) were calculated for cutthroat and brown trout (adults and subadults based on length frequency data) for each site, and then compared within and across sites.

Population estimates

Population abundances were estimated based on a generalized maximum-likelihood removal estimator calculated in Program MARK (White and Burnham 1999). In

previous years, in order to compare to past UDWR estimates more directly, we relied on the Zippin method (based on least-squares regression), which uses only two of the three passes actually completed in our census. In addition to using the data from all three passes, the maximum-likelihood procedure in itself produces a more robust and consistent model and confidence intervals, thus giving us a more reliable indicator of the uncertainty regarding trout population estimates. Estimates were calculated based on an iterative approach, selecting combinations of capture probability and population size until the model that makes the data appear most likely is found.

Whirling disease analyses

For a subsample of cutthroat and brown trout, fish heads from each specimen were removed, frozen, and tested for prevalence of *M. cerebralis* following the polymerase chain reaction method (Hsp PCR; Andree et al. 1998). PCR samples were processed by Pisces-Molecular LLC (Boulder, Colorado).

Fish health condition assessment

Some of the same subsampled fish taken for PCR analysis were also assessed for health and condition using procedures outlined by Goede (1988, 1991). One technician conducted this profile for the 2003-2004 sampling periods.

Fish tagging

In order to better understand the degree of fish movement between sites and determine growth and survival of tagged fish, we marked cutthroat trout and brown trout species at each site with different colored site-specific Floy T-bar anchor tags inserted just posterior to the dorsal fin. Tagged fish were recovered from anglers (creel census and phone returns) and from the annual electroshocking survey in late summer. Informative signs were also placed at the major fishing areas. The USU Fish Ecology Lab's phone number (435-797-3380) was imprinted on the fish tags. Recapture rates were determined over the period July 2003 to July 2004.

Movement—Long-range movement (0.6-34 km) was detected throughout the eight index sites by recapturing tagged individuals in index areas other than those in which they were tagged. Site fidelity was presumed when fish originally tagged at a particular site, were recaptured at that same site. Site fidelity rate was calculated as the number of recaptured fish that were originally tagged at a particular site divided by the number of total recaptures at that particular site. Movement and site fidelity was pooled for recapture years 2003 and 2004.

Growth—Annual growth was determined between the period of initial tagging and subsequent recaptures. Weight gain over a specified interval was used to calculate an instantaneous growth rate (g/g/day) for each individual.

Emigration rates—Site-specific emigration rates for fish tagged in 2002 and recaptured in 2003 were estimated by dividing the number of fish that moved from a specific index site to a specific destination site (also an index site) by the capture probability at that destination-index site. Site-specific capture probabilities were estimated in Program MARK (White and Burnham 1999) for all ages (1 and older) combined. These site-specific emigrant estimates were then summed across the index sites and divided by the total number of tagged fish at that index site, to obtain an emigration rate from a particular index site. Tag loss was set at 15% (Brewin et al. 1995; Ombredane et al. 1998). Three tagged fish that were captured at non-index sites were not included in analysis because three-pass depletion estimates and long-term monitoring were not conducted at those sites.

Survival estimates—To determine age-specific survival rates, cutthroat trout were divided into three age classes: age-1 (ranged from 75-149 mm), age-2 (150-224 mm), and age-3 and older (≥ 225 mm). Rates of apparent survival were then calculated for each age class over two time intervals: (Interval 1) fish that were tagged in 2002 and recaptured between 1 July 2003 and 30 June 2004 and (Interval 2) fish that were tagged in 2002 and 2003 and recaptured between 1 July 2004 and 30 June 2005:

$$S_{Interval1} = (R_{2003} / p_{2003}) / [Tags_{2002} + (Tags_{2002} \times Tag\ Loss\ Rate)]$$

$$S_{Interval2} = (R_{2004} / p_{2004}) / [(R_{2003} / p_{2003}) + (Tags_{2003} + [Tags_{2003} \times Tag\ Loss\ Rate])]$$

where S = survival, R = number of recaptured fish, p = capture probability, $Tags$ = number of tagged fish at large, $Tag\ Loss\ Rate = 0.15$. Survival estimates were adjusted by a tag loss rate of 15% (Obredane et al. 1998; Brewin et al. 1995). Apparent survival was then estimated by averaging survival estimates for these two time intervals; a range was determined by the upper SE bound of the highest and lower SE bound of the lowest survival estimate for each size class.

Environmental variables

Sampling of river water for physical and chemical characteristics was generally conducted prior to fish sampling.

Temperature—Temperature at each site was recorded hourly using temperature loggers (Onset Stow Away) set in streams, generally from May through October.

Discharge—Discharge was measured using the recommended method of the U.S. Geological Survey. Thus, we measured depth and mean water column velocity at 20-30 locations along a cross-sectional transect at each site using a Marsh-McBirney Flow Mate 2000 electromagnetic flow meter. In addition to measuring discharge, we estimated stage-discharge relationships for Twin Bridges, Forestry Camp, Red Banks, and Franklin Basin based on water surface elevation recorded at Franklin Basin on the date of all discharge measurements; thus, we created a stage-discharge curve for use in the estimation of flow based only on the observed water surface elevation at the Franklin Basin bridge. All curves were fit using least-squares regression using SAS statistical software. Finally, in order to assess the flow variability throughout the year, we reconstructed the hydrograph for 2004 using daily flow measurements made at USGS gage number 10109000, immediately above First Dam.

Nutrients—Water samples were collected in dark sample bottles at four sites in the Logan River drainage. Bottles were first acid washed with 1 N HCl and rinsed three times with on-site stream water. Samples were stored in an ice cooler in the field and frozen in the lab. Frozen samples were analyzed within three months by High Sierra Water Lab (Truckee, California).

Periphyton—Chlorophyll *a*, extracted from periphyton, was used as an index of productivity. For each sample site, 15 rocks were blindly selected. Rocks were scrubbed with a brush into a basin until all algae was removed. Total volume of scrubbate was determined for each rock. A 5- to 25-mL subsample of each rock's scrubbate was filtered and frozen. Rock surface area was determined by cutting out a rock tracing on a piece of waterproof paper. Each rock cutout was weighed to the nearest 0.0001 g. A standard curve was constructed by cutting out pieces of paper of known area and determining the weight of those on the same balance, then graphing the paper area vs. weight and determining the relationship between the two. This standard curve relationship was used to determine the area of the unknown rocks. Chlorophyll *a* was extracted in the dark for 24 h at room temperature. From the extract, three 6-mL aliquots were analyzed fluorometrically. Chlorophyll *a* concentrations were then calculated using the formula

$$\mu\text{g cm}^{-2} = \frac{(\text{Fluorometer reading } (\mu\text{g L}^{-1}) * \text{extraction volume (mL)} * \text{scrubbate volume (L)})}{(\text{volume filtered (mL)} * \text{rock area (cm}^2\text{)})}$$

Substrate—Substrate particles were collected randomly at approximately five located within three sites by walking through a transect perpendicular to the shoreline. Gravel size distribution was assessed using a gravelometer, where a minimum of 100 blindly selected gravels were sized. Percent fine sediments (< 10-mm diameter rock particles) was calculated.

Other physical variables—In addition to temperature information from data loggers set in selected index sites, temperature of surface water, measured with a hand-held thermometer at the time fish were sampled, was recorded. Water conductivity ($\mu\text{S}/\text{cm}$) and pH-level were recorded with an Oakton model 10 pH/Conductivity meter at three index sites. A water sample was also taken in a plastic container and allowed to reach equilibrium with air temperature. Turbidity (NTUs) was measured from this sample with a LaMotte model 2020 turbidity meter.

RESULTS

Field sampling

Fish collections and population estimates

Bonneville cutthroat trout, brown trout, rainbow trout, brook trout, and mountain whitefish were sampled during stream surveys in the Logan River drainage in summer 2004. We also captured sculpin at most sites and common carp and white suckers at the lowermost (Lower Logan) site. Based on length frequency histograms, cutthroat trout appeared to represent at least four age classes, while brown trout represented at least five age classes (Figure 1.2). Eighty-one mountain whitefish were captured, mainly at the Lower Logan site, and 101 brook trout were captured at a site on Spawn Creek, above a large beaver dam (Figure 1.2). Based on depletion population estimates, abundance of cutthroat trout, brown trout, and mountain whitefish varied considerably across sites in the Logan River (Figures 1.3, 1.4, and A5). Electrofishing catches were lower in 2004 versus previous years. Numbers of cutthroat trout per km decreased at three sites, remained the same at one site, and increased at two sites (Figure 1.3). Numbers of brown trout per km generally decreased slightly, or remained the same, depending on site as compared to previous estimates (Figure 1.4). The following abundance summaries by site are based on maximum-likelihood depletion population estimates.

Franklin Basin—Surveys indicated that cutthroat trout abundance has fluctuated greatly since 2001 (Figure 1.3). In 2004, we captured 99 cutthroat trout ranging from

79 to 317 mm TL and 4.4 to 327 g for a population estimate of approximately 1052 fish/km (95% CI = 1009 – 1195). Unlike past surveys, we did not capture fish less than 50 mm, representing young-of-the-year (age-0) fish. No brown trout and only three brook trout were captured at this site, precluding a population estimate.

Red Banks—Cutthroat trout abundance at this site has decreased significantly (Figure 1.3). Most of the fish captured were cutthroat trout (n = 171) resulting in an abundance estimate of nearly 845 fish/km (95% CI = 843 – 879). Eight brown trout were captured, yielding a population estimate of 39 fish/km; similar to estimates obtained from past surveys (Figure 1.4). As only two whitefish (445 and 455 mm TL) were captured, a population estimate was not calculated.

Forestry Camp—We captured 196 cutthroat trout at this location, more than at any other sampling site, providing a population estimate of 1063 fish/km (95% CI = 1017 – 1168; Figure 1.3). Cutthroat trout abundance has decreased steadily since 2001 (Figure 1.3). Only eight brown trout (size range = 87 – 300 mm TL) were captured.

Twin Bridges—Brown trout (338 fish/km) were more abundant than cutthroat trout (158 fish/km) at this site, and abundance of both species has remained stable since 1991 (Figures 1.3 and 1.4). We captured 77 brown trout (size range = 121 – 389 mm TL), 33 cutthroat trout (111 – 325 mm TL), and four whitefish (73 – 453 mm TL; Figure A5).

Third Dam—As in past surveys, Third Dam was the only site where rainbow trout (n = 5) and albino rainbow trout (n = 3) were captured: ranging from 201 - 325 mm. Brown trout were abundant (1510 fish/km; 95% CI = 1491 – 1562; Figure 1.4) at this location, whereas abundance estimates of cutthroat trout (70 fish/km) were much lower (Figure 1.3). We captured 296 brown trout (ranging from 40 – 393 mm TL) and 14 cutthroat trout (104 - 301 mm (Figure 1.2). Thirteen whitefish were collected – one was a juvenile (75 mm TL), the remainder ranged from 276 - 453 mm – producing a population estimate of 13 fish/km (Figure A5).

Lower Logan—Brown trout dominated this section of the river (589 fish/km; 95% CI = 574 – 641); however, abundance has decreased dramatically since our first survey at this site in 2001 (2317 fish/km; Figure 1.4). As in past years, no cutthroat trout were captured at this site. One hundred sixty-nine brown trout were captured ranging 57 – 375 mm TL, representing at least four size classes. More whitefish were captured this year (n = 61) than in past years: 43 were less than 101 mm TL and the remainder ranged from 255 – 389 mm TL. Whitefish abundance (24 fish/km; 95% CI = 24 – 32) in 2004 has decreased vastly since 2001 (1274 fish/km; Figure A5); however, it is important to note that whitefish are quite sensitive to sampling.

Temple Fork—As in 2003, a large beaver dam in the center of our study section (used in 2001 and 2002) again forced us to modify our study section. One 100-m section was surveyed above the beaver dam (upper site), and another 62-m section was surveyed from the beaver dam to the confluence with the Logan River mainstem (lower site). In the upper 100-m section, we captured 17 cutthroat trout and 4 brown trout, and in the lower 62-m section, we captured 15 cutthroat trout and 4 brown trout, much fewer than in all previous years. An abundance estimate was only calculated for cutthroat trout by combining captures from upper and lower sites (199 fish/km; 95% CI = 198 – 247; Figure 1.3). This was the only site at which cutthroat trout less than 60 mm were captured. Precisely as in 2003, 86% of captured brown trout were less than 100 mm.

Right Hand Fork—As in past surveys, only brown trout were captured ($n = 183$); however, this compares poorly to 316 captured in 2003 at this same site. The population has declined from nearly 3000 fish/km in 2001 to 1814 fish/km (95% CI = 1743 – 1982; Figure 1.4) in 2004. Size structure of the population remained similar to past years with brown trout ranging from 47 – 321 mm TL. A third of the captured brown trout were less than 100 mm TL.

Overall, if we consider just our (Utah State University) fish survey data since the 2001 survey, cutthroat trout population estimates have decreased significantly at one site (Red Banks) and show apparent downward declines (but statistically insignificant) at two other sites where they occur. Similarly, brown trout demonstrate apparent downward declines at five of the seven sites where they occur, with dramatic (three-fold) declines at the Lower Logan site. However, our estimates are similar to past UDWR fish survey data, suggesting no marked decline of either species from 1990's levels. Due to beaver activity at the Temple Fork site, it is inappropriate to compare 2001 – 2002 population estimates to estimates from 2003 – 2004. Although whitefish appear to have declined, we suspect that this is a site-specific artifact of electroshocking.

Condition analysis

Cutthroat trout—Condition, as measured by Fulton's K, has varied greatly since the study began in 2001. In 2004, condition of adult and subadult cutthroat trout increased slightly from 2003 (Figure 1.5). In general, cutthroat trout at Forestry Camp were in the best condition, while fish at Third Dam exhibited lowest condition. Subadult cutthroat trout average condition (± 1 SE) was highest at Red Banks (1.09 ± 0.02) and Forestry Camp (1.06 ± 0.01), and lowest at Third Dam (0.88 ± 0.07 ; Figure

1.6). Adult cutthroat trout average condition ranged from 0.93 ± 0.02 at Third Dam up to 1.06 ± 0.01 at Forestry Camp. Cutthroat trout from the tributaries and mainstem exhibited similar condition.

Brown trout—Condition of adult brown trout has fluctuated little since 2001; however, condition of subadult brown trout has decreased significantly since 2001 (Figure 1.5). Average condition of subadult brown trout ranged from $0.93 (\pm 0.02)$ at Lower Logan to 1.09 ± 0.06 at Red Banks (Figure 1.7). Adult brown trout average condition ranged from 0.94 ± 0.02 at Lower Logan to 1.04 ± 0.02 at Twin Bridges. Brown trout from the tributaries and mainstem exhibited similar condition.

Fish tagging

Nearly 900 cutthroat trout and over 1000 brown trout were tagged from 2002 to 2004. Recapture rates of tagged cutthroat trout during the annual electrofishing survey ranged from 6.3% at Temple Fork up to 30.5% at Red Banks, with an average rate (all sites combined ± 1 SE) of 20.2% (± 4.5). Average recapture rate for brown trout was 18.3 % (± 6.5), and varied from 0% at Temple Fork to 34.5% at Third Dam. The Temple Fork site has changed greatly since 2002 (initial tagging season) due to beaver activity near the confluence with the Logan River mainstem.

Table 1.2. Number of cutthroat trout tagged and recaptured by sample site in the Logan River, Utah, 2002-2004. Dashes (--) indicate non-applicability.

| Location | 2002 | 2003 | Total # | Total # Recaptured 2003-2004 | Total # Sedentary | Total # of movers to site |
|--------------------------------|------|------|---------|------------------------------|-------------------|---------------------------|
| Franklin Basin | 128 | 32 | 160 | 15 | 15 | 0 |
| Red Banks | 198 | 22 | 220 | 67 | 65 | 2 |
| ^a Little Bear Creek | -- | -- | -- | 2 | -- | 2 |
| ^a Tony Grove Creek | -- | -- | -- | 1 | -- | 1 |
| Forestry Camp | 190 | 2 | 192 | 54 | 54 | 0 |
| Temple Fork | 101 | 10 | 111 | 7 | 6 | 1 |
| Twin Bridges | 20 | 20 | 40 | 9 | 8 | 1 |
| Third Dam | 3 | 0 | 3 | 0 | -- | -- |
| <i>Total</i> | 640 | 86 | 726 | 155 | 148 | 7 |

a. No fish were initially tagged in Little Bear and Tony Grove creeks. These sites are not index sites. Cutthroat trout were encountered during surveys to collect samples for whirling disease testing.

Movement-- Most cutthroat trout remained sedentary. Rates of sedentary fish were 100% at Franklin Basin and Twin Bridges and was lowest at Temple Fork (85.7%) with an average sedentary rate of 95.8% (SE = 2.6%; Figure 1.8). Only one tagged brown trout moved, while 150 brown trout remained sedentary (99.0% \pm 1.0%). Long-range movement of cutthroat trout ranged from 630 m to 9.3 km. Cutthroat trout movement varied by site, both upstream (55% of movement) and downstream, from 2002 to 2004 (Figure 1.9). Only one brown trout moved; upstream 3 km from the Lower Logan site into Logan City (Figure 1.9).

Growth--On average (\pm 1 SE), tagged cutthroat trout gained 37.7 g (\pm 2.9) over a one-year period (July 2002 - July 2003) at first recapture. Cutthroat trout that were again recaptured (second recapture on same fish) one year later (July 2004) gained 36.1 g (\pm 4.3). Cutthroat trout that were tagged in July 2002 and first recaptured after two years (in July 2004) grew an average 68.5 g (\pm 11.2). Cutthroat trout tagged in 2003 and recaptured in 2004 grew an average of 37.1 g (\pm 7.5).

Tagged brown trout (n = 102) gained an average of 71.7 g (\pm 5.5) from July 2002 - July 2003, and some of these same fish (n = 42) gained an average of 73.3 g (\pm 8.8) upon second recapture in July 2004. As with cutthroat trout, weight gain of brown trout tagged in 2003 and recaptured in 2004 was greater (92.4 \pm 13.3) than during 2002 - 2003.

Although net-average annual growth (both length and weight gain) was greater for brown trout versus cutthroat trout at all recapture events, growth rates (g/g/day) of cutthroat trout were somewhat higher or similar to brown trout growth rates (Figure 1.10). Growth rates were higher over the period July 2002 to July 2003 as compared to the period July 2003 to July 2004, for both cutthroat and brown trout (Figure 1.10).

Emigration rates--Site-specific emigration rates for tagged cutthroat trout varied greatly by sample site; rates were lowest at Red Banks and highest at Forestry Camp (Table 1.3). Rates increased only slightly when tag loss was incorporated. Only one brown trout moved, therefore emigration rate was low (Table 1.3).

Survival estimates-- Cutthroat trout average apparent survival was similar for age-2 and older fish (Table 1.4). Survival rates for age-1 fish could not be estimated due to low numbers of tagged age-1 fish (n = 33) and low recapture rates of those same fish in 2003 (n = 1) and 2004 (n = 1).

Table 1.3. Emigration rates (number of fish per year) for cutthroat trout and brown trout at sites on the Logan River where movement information was available, 2002 and 2003.

| Species | Emigration from site | Rate | Rate considering tag loss |
|------------------------|----------------------|--------|---------------------------|
| <i>Cutthroat trout</i> | Forestry Camp | 0.0318 | 0.0328 |
| | Red Banks | 0.0051 | 0.0052 |
| | Temple Fork | 0.0185 | 0.0191 |
| <i>Brown trout</i> | Lower Logan | 0.0062 | 0.0073 |

Table 1.4. Average apparent survival rates for age-2 and older, tagged and recaptured cutthroat trout in the Logan River, Utah, 2002-2003.

| Age class | Average survival with tag loss | Range |
|-----------|--------------------------------|---------------|
| age-2 | 0.347 | 0.255 – 0.426 |
| ≥ age-3 | 0.338 | 0.159 – 0.519 |

Ageing analysis

We aged a select subset of scales from cutthroat trout (79 - 298 mm TL) captured in 2004. This size range was selected to pinpoint size-range differentiation between age-1, age-2, and age-3 fish. Size-at-age analysis shows distinct size ranges for age-1, age-2, and age-3 cutthroat trout (Figure 1.11).

Whirling disease analyses

Cutthroat trout—Clinical signs of whirling disease such as black tail or deformities were observed in approximately 1% of cutthroat trout handled. However, PCR assays for *M. cerebralis* indicated the parasite was present in all mainstem reaches tested and in two tributaries: Temple Fork and Spawn Creek. Despite the widespread distribution of *M. cerebralis*, the prevalence of infection on cutthroat trout varied greatly, ranging from 18% of adults at Franklin Basin to 100% of adults at Twin Bridges (Figure 1.12). The average number of cutthroat trout testing positive for *M. cerebralis* across sites has decreased slightly in 2004 (Figure 1.13); however, two

sites were not tested in 2004, which would likely influence the average. More adults tested positive versus subadults (< 150 mm TL), 64% and 59.6%, respectively (Figure 1.12).

Brown trout—Since 2001, *M. cerebralis* has not been detected in brown trout from Right Hand Fork. Percentage of brown trout that tested positive ranged from 45% at Twin Bridges to 55% at Third Dam (Figure 1.14). The average number of brown trout testing positive decreased slightly in 2004 (Figure 1.13); however, two sites were not tested in 2004, which would likely influence the average. More adults tested positive versus subadults (< 180 mm TL), 44.4% and 31.2%, respectively.

Other salmonids—Prevalence of *M. cerebralis* was not tested in rainbow trout, mountain whitefish, or brook trout due to lack of funding. A subsample of these fish that were taken in 2004 is being held frozen at the Fish Ecology Lab at Utah State University and will be analyzed if funds become available.

Fish health condition assessment

Health and condition (as based on UDWR HCP assessment) was assessed on 25 cutthroat trout and 15 brown trout collected from 28 July to 4 August 2004 at Franklin Basin, Twin Bridges, and Spawn Creek (Temple Fork) sites. Hemorrhagic eyes were observed in 0% of fish, versus 26% in 2003 and 0% in 2002 (Budy et al. 2004). As in past years, no gill or pseudobranch abnormalities were observed, and in 2004, no hemorrhaging of the thymus was seen. Eighty percent of trout had > 50% fat coverage of pyloric ceca. Red coloration of the spleen was observed in 64% of cutthroat trout and 80% of brown trout, lower rates than in 2003. As in past years, no trout had inflammations in the hindgut. No swollen kidneys were observed. Eighteen percent of trout had “non-red” livers, down from 30% in 2003. Bladders were empty in 97% of fish. Seven sampled brown trout were immature, 63% were females, and 37% were males. Four sampled cutthroat trout were immature, 62% were females,, and 38% were males. While no brown trout displayed malformed pectoral fins or opercles, several cutthroat trout captured at Franklin Basin were deformed: one had a deformed caudal peduncle, three had deformed caudal fins, and two had deformed opercles.

Environmental variables

Temperature—As in past years, average daily temperatures were coolest in the highest elevation site (Franklin Basin) and warmest at the lowermost site (Lower Logan; Figure 1.15). Also, average summer (June-September) temperatures at most

sites (except for Franklin Basin) were close to or within the ideal range (10 to 13 °C) for growth of *T. tubifex*, the secondary host for *M. cerebralis*. From 2001-2004, average summer temperatures at the Lower Logan site were above that range (Figure 1.16; Figure A2). In 2004, mid-summer temperatures at Third Dam approached the ideal 15 °C for triactinomyxon (TAM) production (Figure 1.15). On the other hand, temperatures between 13 and 17 °C have been correlated with higher *M. cerebralis* infection rates in other studies. Our 2004 data indicate that mid-summer temperatures at Red Banks, Forestry Camp, Twin Bridges, and Third Dam, and early and late summer temperatures at Lower Logan fell within this category. Temperatures at Franklin Basin were generally below ideal for TAM production, *T. tubifex* growth, and the temperature range that has been correlated to high infection rates (Figure 1.15).

Discharge—Average and peak flows were similar to those recorded at monitoring sites in 2003 (Figure 1.17). We estimated stage-discharge relationships for the four mainstem sites that are not influenced by irrigation diversions using a regression model (Figure A3). Finally, the 2003 Logan River hydrograph was characterized by three spikes from May to mid June with a peak flow in late May (near 550 cfs) followed by a rapid decline to base flow in late June (Figure 1.18). This contrasts with a peak flow of over 700 cfs in June 2003 (Budy et al. 2004).

Nutrients—Nitrogen (ammonia, nitrate-nitrite, and total kjeldahl) and phosphorus (soluble reactive, dissolved, and total) concentrations varied by site (Figure 1.19). Total kjeldahl nitrogen (TKN; 0.274 mg/L) and total phosphorus (TP; 0.037 mg/L) were highest at Franklin Basin, the headwater site, and similarly high at Spawn Creek, a tributary site.

Periphyton—Analysis of chlorophyll *a* is ongoing.

Substrate—Size distribution of particles ranged across three sampled sites. The headwater Franklin Basin site had the highest number of small (< 8 mm) and large (> 300 mm) particles (Figure 1.20). At the Twin Bridges and Third Dam sites, over 81% and 65%, respectively, of particles were \geq 64 mm. Percent fines was highest at Franklin Basin, followed by Third Dam, and lowest at Twin Bridges (Figure 1.21a).

Other physical variables—Values of *pH* ranged from 6.5 at Franklin Basin to 8.4 at Twin Bridges (Figure 1.21b). Conductivity was similar at all sites, ranging from 327 to 353 μ S/cm (Figure 1.21c). Turbidity was highest at Twin Bridges (1.9 NTU) and was similarly low at Third Dam (0.40 NTU) and Franklin Basin (0.35 NTU; Figure 1.21d).

DISCUSSION

Since *M. cerebralis* was first detected in the Logan River in 1998, its range has increased throughout the mainstem and most of the tributaries. Of the sites we sample regularly, Right Hand Fork is the only site that consistently tests negative for the presence of *M. cerebralis*. The average number of cutthroat trout testing positive for *M. cerebralis* has increased annually by about 10-20% per year through 2003 with a slight plateau in 2004 (Note, however, that some previously highly positive sites were not tested in 2004). Consistently, more adults test positive as compared to juveniles, and prevalence is higher at mainstem sites as compared to tributary sites. These results suggest that the 2001 - 2002 based-relationship between increasing prevalence and temperature in De la Hoz Franco and Budy (2004) still applies in the Logan River (i.e., the colder tributaries have lower prevalence). As discussed in greater detail in Chapter 5, these results suggest that changes to stream temperature or discharge, either natural or anthropogenic, could alter the spread and impact of *M. cerebralis* in mountain streams.

Despite the high rates of infection, we rarely observe clinical signs (e.g., deformities, black tail) of the disease. Condition values (Fulton's K) for cutthroat trout have fluctuated around 1.0 over the past four years and thus generally paralleled what has been observed elsewhere (e.g., Hepworth et al. 1999). In 2004, however, we did detect a downward decline in population abundance at four of the six sites where cutthroat trout occur. While the short time series used to detect trend (~ 4 years) somewhat limits our ability to determine the future status of this population with certainty (Morris and Doak 2002), a precautionary approach to the management of this protected species is recommended given the possibility of a downward trend (Caswell 2000).

In 2004, tagging data accumulated and allowed us, in combination with scale ageing, to develop rigorous estimates of age- (or stage-) specific survival and growth. These estimates indicate that both growth and survival of cutthroat trout in the Logan River system is quite high relative to what has been observed elsewhere. In a review of available information and expert opinion, Hildebrand (2003) estimated survival at 0.23 and 0.35 for age-2 and older cutthroat trout, noting that these estimates were thought to be high. In contrast, we estimate survival rates of 0.347 and 0.338 for these same age groups, respectively. Based on his transition probabilities (the probability that a fish will stage based on its growth), it appears that subadult and adult cutthroat trout in the Logan River also experience higher growth rates than were previously thought,

but the data are not available for a direct comparison. These results suggest that if whirling disease is causing a population-level decline, it is occurring at the age-0 to age-1 life stages, which corresponds with what is known about the biology and effect of the parasite (i.e., juveniles are more susceptible).

A greater synthesis of fish abundance, disease, and abiotic effects is provided in Chapter 5.

FUTURE

Monitoring

Monitoring of salmonid populations for abundance, distribution, and disease will continue in 2005, but at a reduced rate to reflect funding reductions. Disease analyses will occur at three of the eight index sites with fewer individuals tested per site. Abundance and distribution sampling and analysis will be the same as completed during the first four years of monitoring.

As part of continuing research effort funded by the Utah State University Water Initiative, in 2005, we will also sample three index sites on the Bear River, some new sites in the Blacksmith Fork drainage, and some additional factors at three of our long-term index sites on the Logan River. The objectives and general approach for that work is as follows. *Objective 1:* Document and understand the abundance and distribution of trout in the Bear and Logan rivers (expanding a previous project from the Logan River into the Bear River proper). We will sample the fish community, the invertebrate community, and primary production at three sites in each river, ranging from the upper headwaters down to the lower, more degraded areas in the valley. *Objective 2:* Measure and evaluate the physical factors (temperature, discharge, etc.) that act to determine fish abundance, distribution, and health (e.g., disease, see De la Hoz Franco 2003). Fish sampled during this monitoring will be used to estimate abundance, will be evaluated for whirling disease (PCR analysis), and will undergo health condition profiling. *Objective 3:* Use stable isotope ratios to develop an index of anthropogenically-derived nitrogen available at all trophic levels and to provide information on food web dynamics. Tracking nitrogen helps describe the importance and influence of water quality and land-use, and may be especially important for understanding differences in abundance and fish health at sites of varying habitat quality (Thompson and Luecke, *unpublished data*). Fish tissue samples, invertebrates, and periphyton will be analyzed for isotopic content, a measure of long-term diet composition and nutrient input. Stomach samples will be evaluated for short-term dietary composition. Temperature, discharge, turbidity, conductivity, and

substrate will be measured monthly from May through October. Discharge and nutrient input, as key variables in many hypotheses about watershed function, were noted as important factors to measure and evaluate during discussions of “science questions and hypotheses” to be addressed in the Utah State University, Water Initiative, Bear River Laboratory Watershed. Monitoring data and research results will be synthesized in combination with results from the Logan River long-term monitoring project. Measures of periphyton, invertebrates, flow, turbidity, substrate, and temperature (described above) will be related to fish abundance, distribution, and health as well as land use and stream habitat quality. Ultimately, we will build a mathematical model to summarize the combined effects of biotic and abiotic factors in determining the present and future status of endemic cutthroat trout in these rivers specifically and which may provide insight into the status throughout their range.

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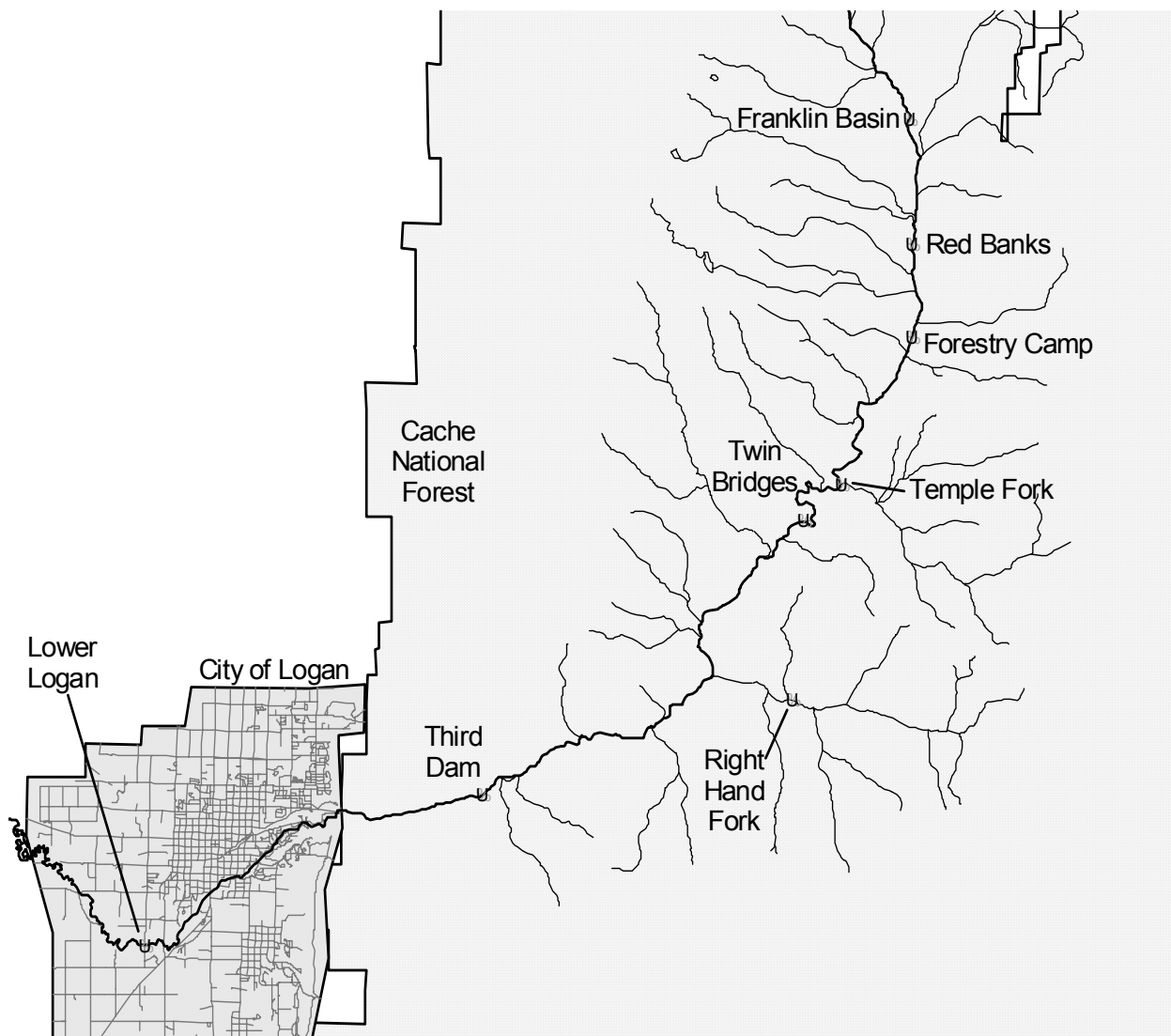


Figure 1.1. Map of the Logan River and eight long-term index sites.

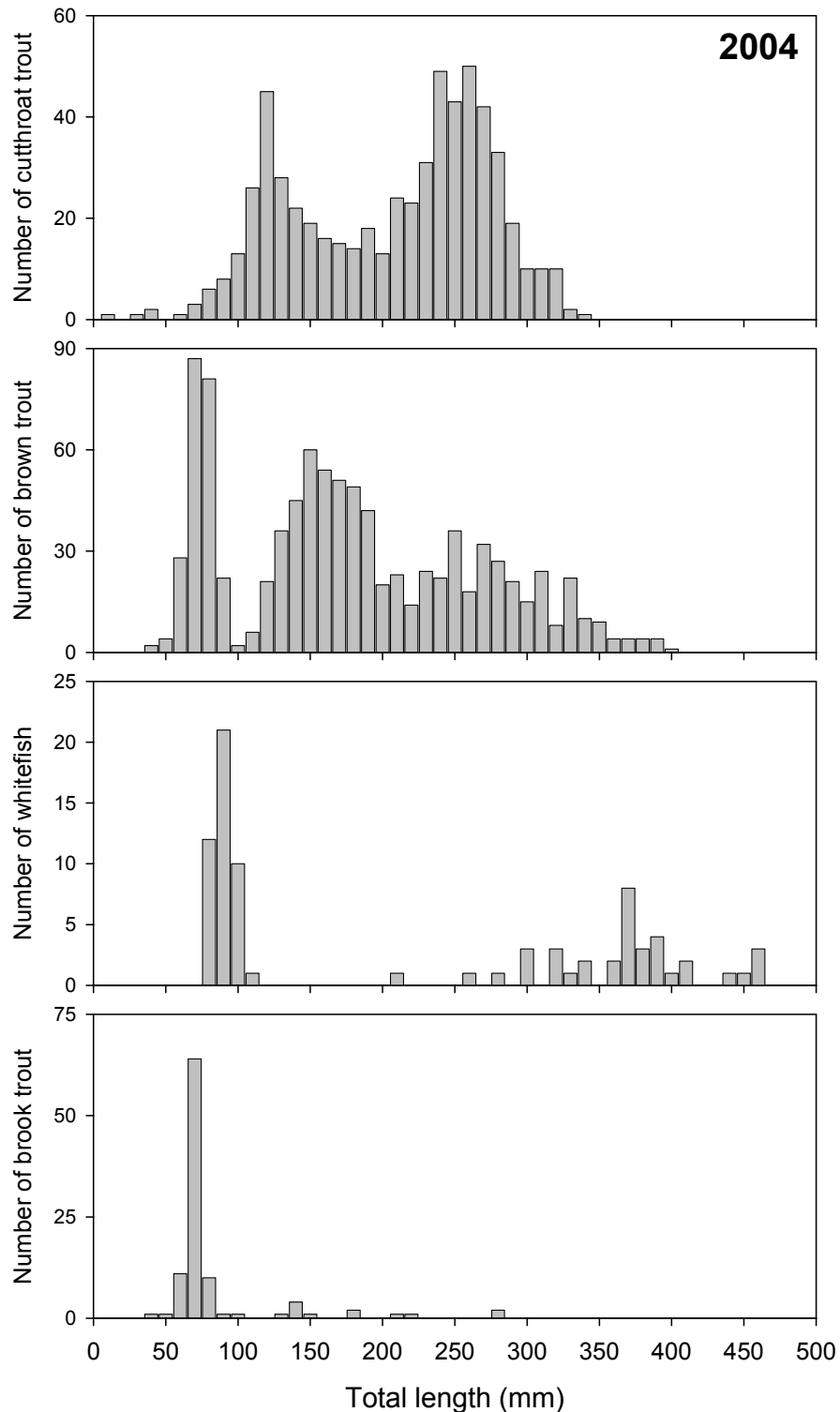


Figure 1.2. Length frequency distributions for cutthroat trout, brown trout, mountain whitefish, and brook trout captured by electrofishing at six sample sites along the Logan River and three tributaries, 2004. All sample sites are combined. Note changes in y-axis scales.

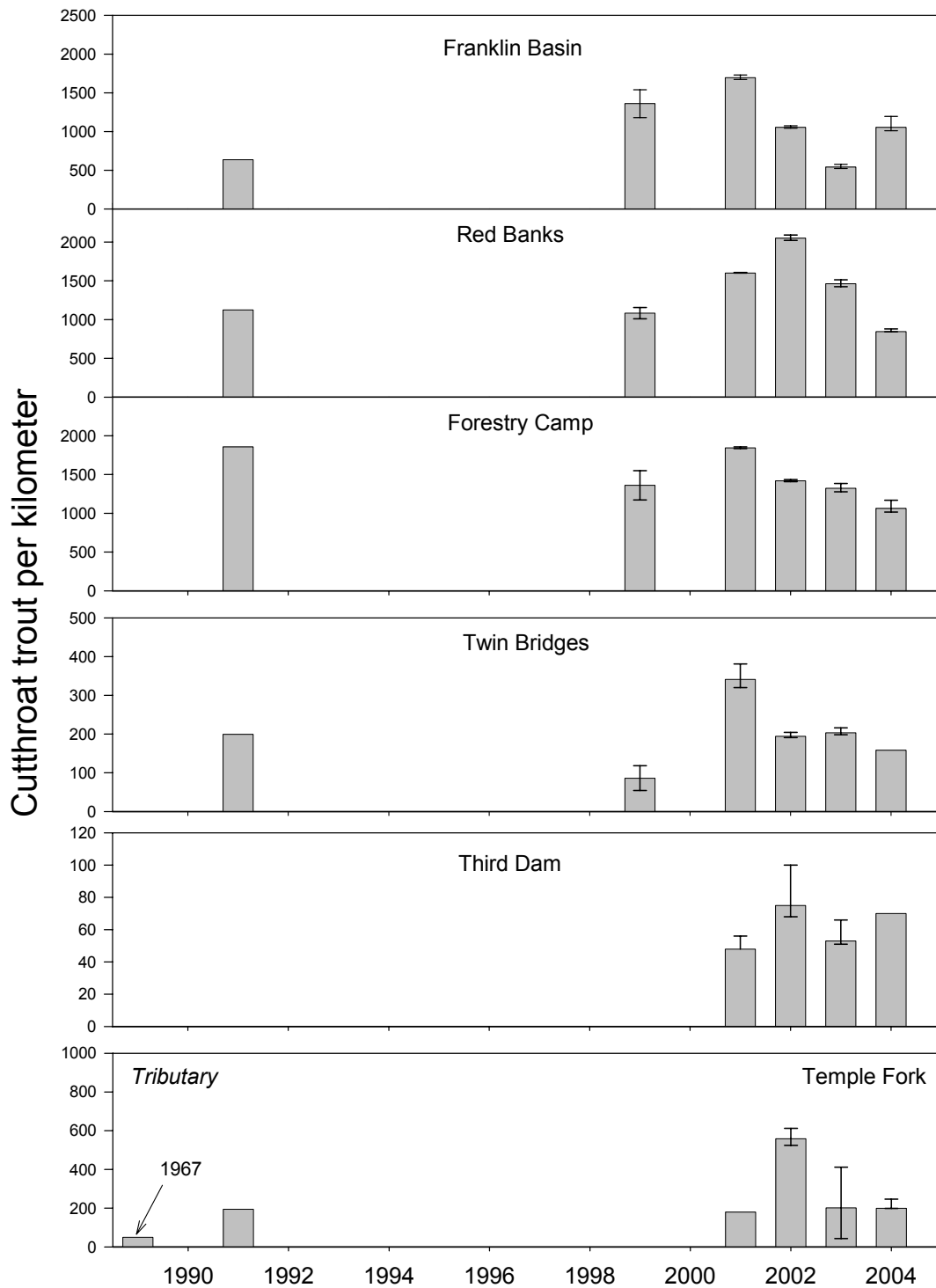


Figure 1.3. Population estimates for cutthroat trout at seven sites on the Logan River, Utah based on the maximum-likelihood removal method in Program MARK (2001-2004 data) and a modified Zippin depletion method (1967-1999 data). Error bars represent 95% confidence intervals (2001-2004) or ± 2 standard errors (pre-2001 data). Note large changes in y-axes.

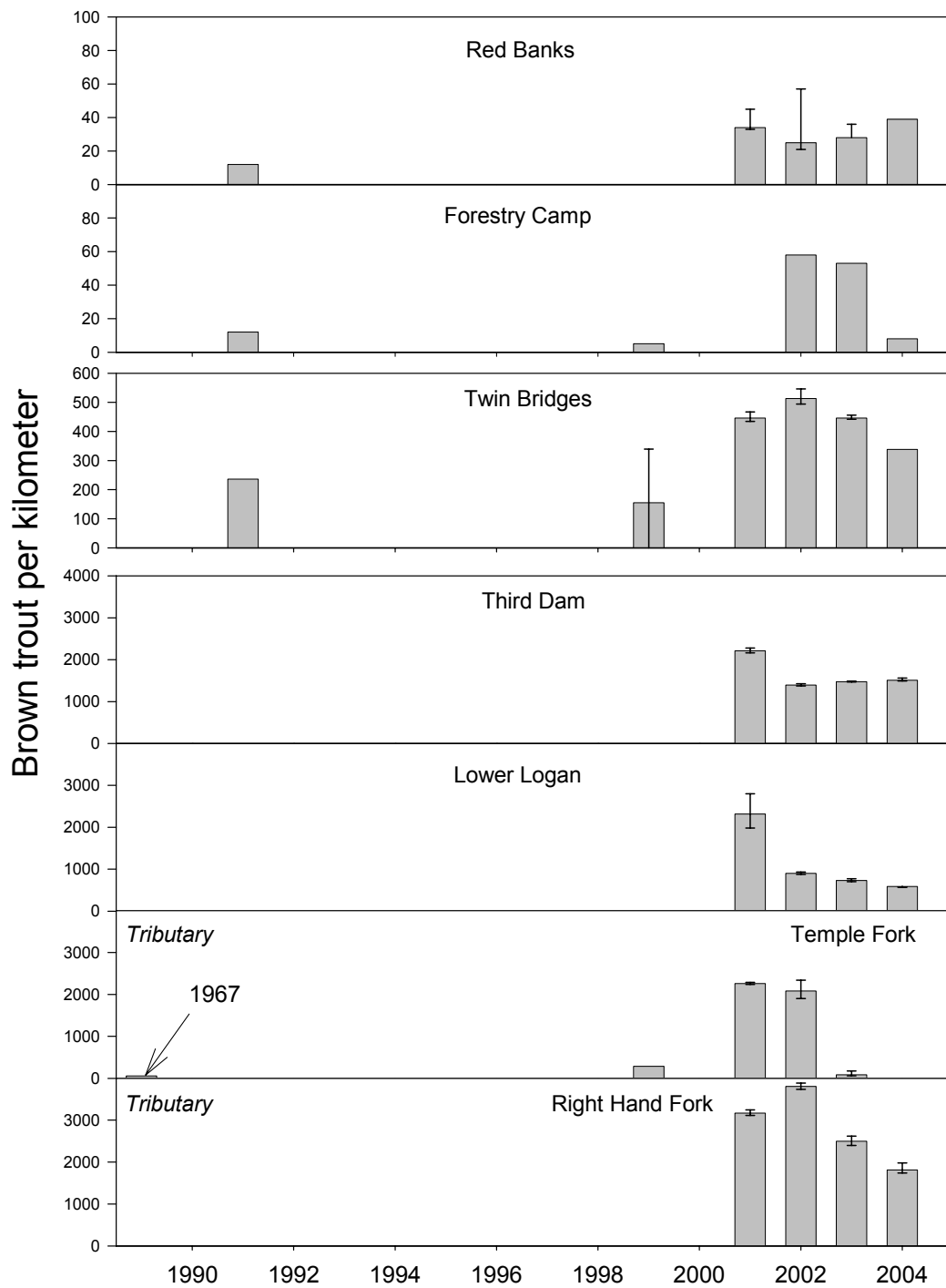


Figure 1.4. Population estimates for brown trout at seven sites on the Logan River, Utah based on the maximum-likelihood removal method in Program MARK (2001-2004 data) and a modified Zippin depletion method (1967-1999 data). Error bars represent 95% confidence intervals (2001-2004) or ± 2 SE (pre-2001 data). Note large changes in y-axes.

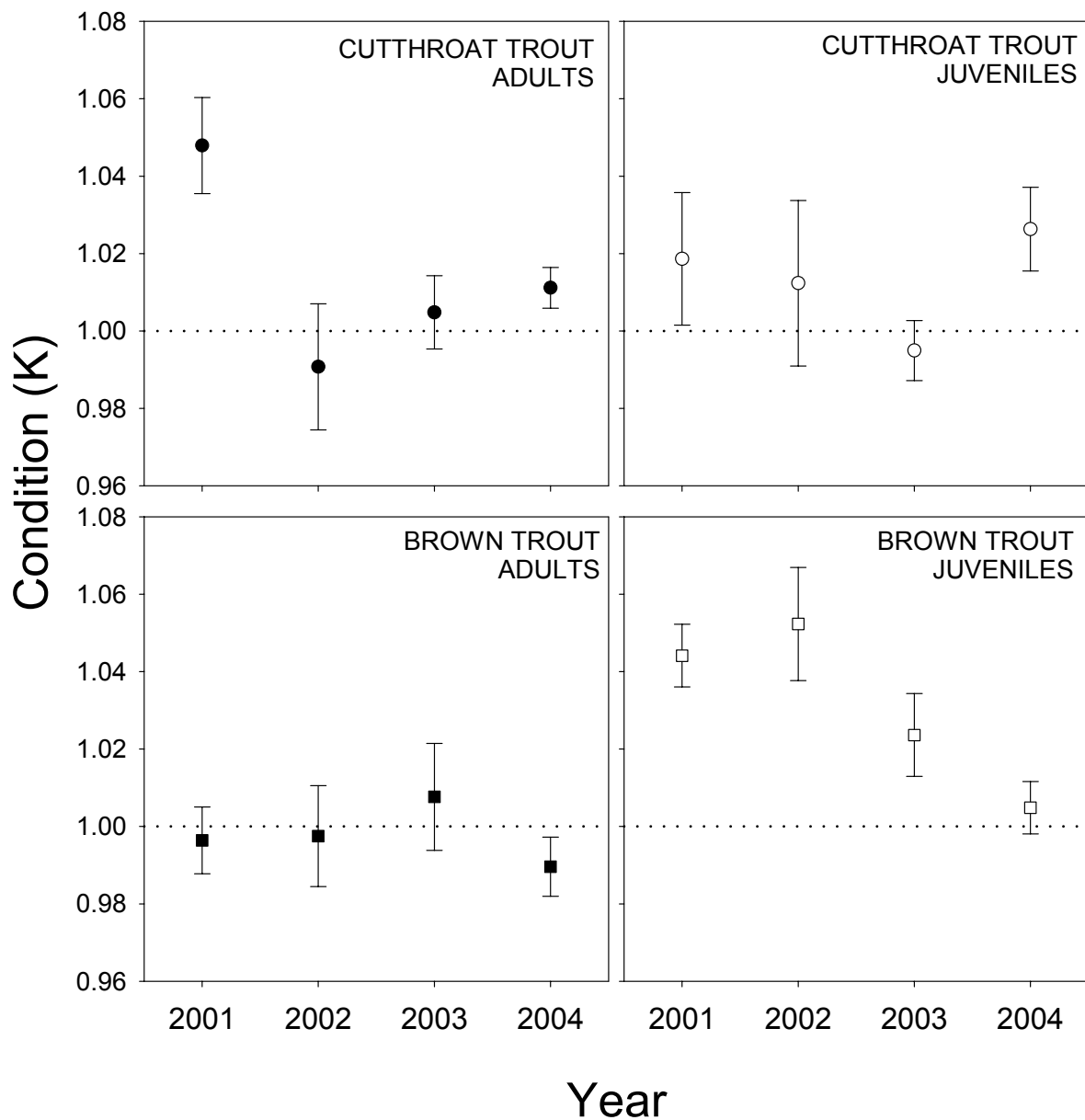


Figure 1.5. Annual average condition (Fulton's K) of adult and subadult cutthroat trout (top panels) and brown trout (bottom panels) captured in the Logan River and two tributaries, 2001-2004. Error bars represent ± 1 SE. $K = 1$ is simply a reference line.

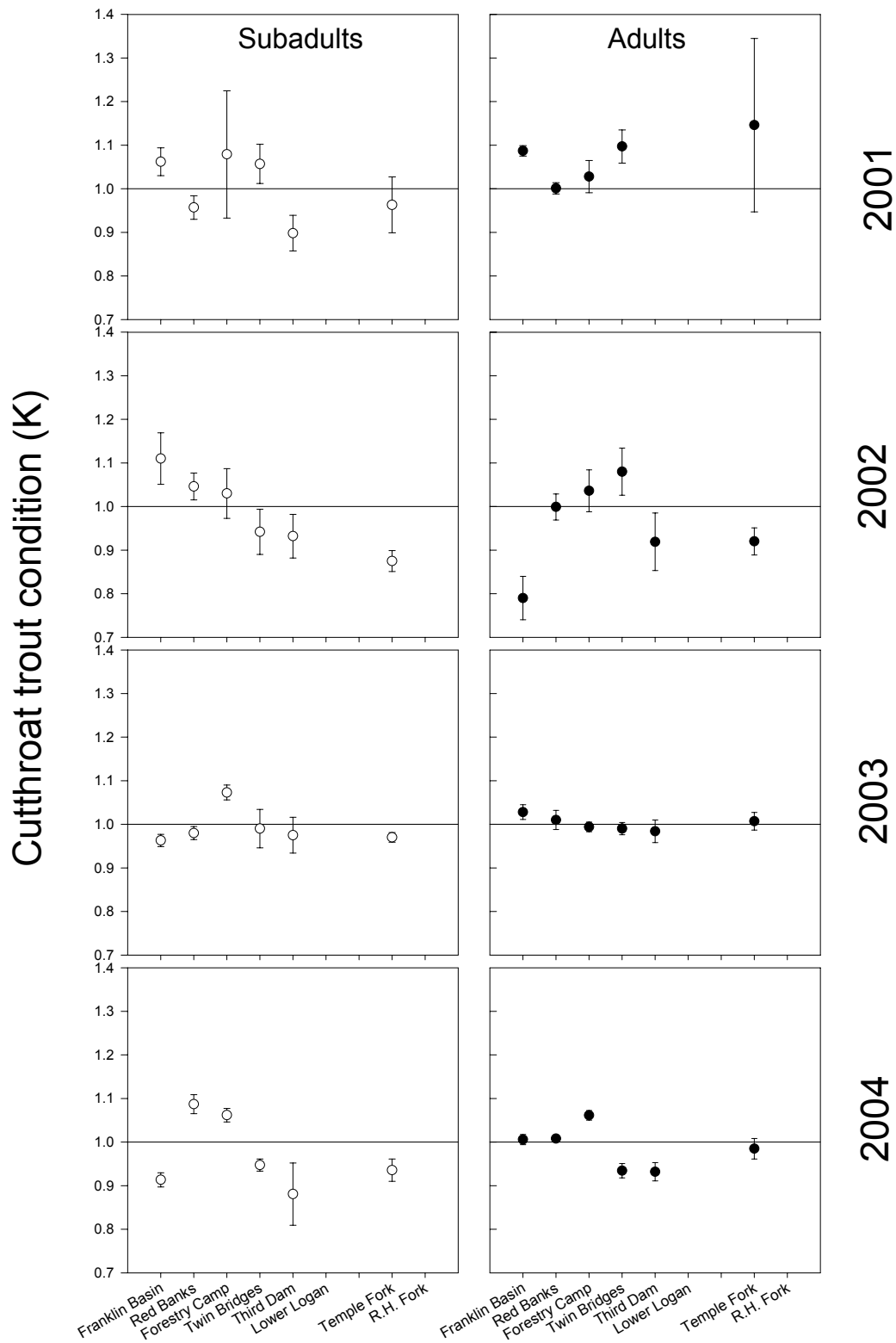


Figure 1.6. Condition (Fulton's K) of subadult (left panels) and adult (right panels) cutthroat trout captured in the Logan River and two tributaries, 2001-2004. Error bars represent ± 1 SE. $K = 1$ is simply a reference line.

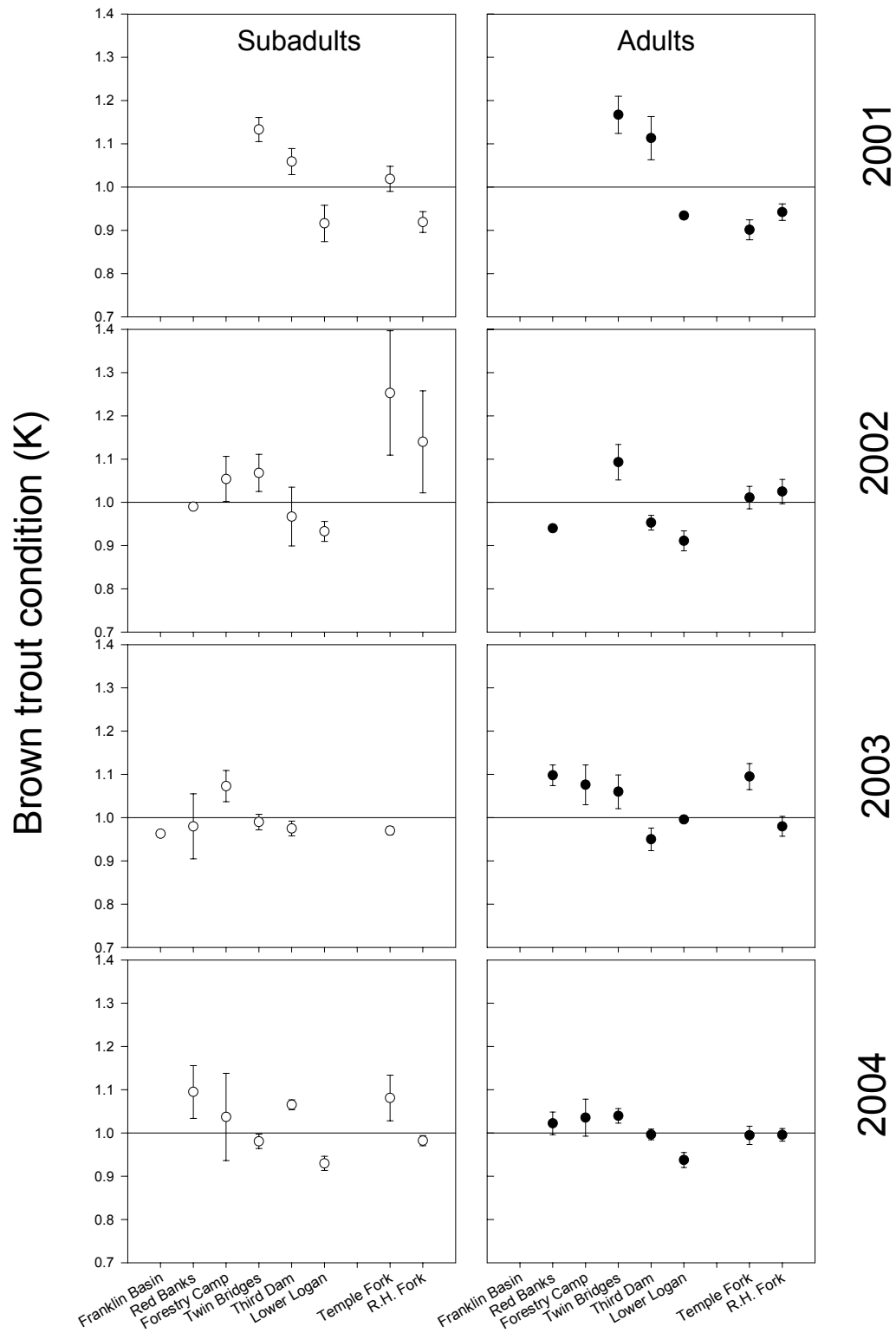


Figure 1.7. Condition (Fulton's K) of subadult and adult brown trout captured in the Logan River and two tributaries, 2001-2004. Error bars represent ± 1 SE. $K = 1$ is simply a reference line.

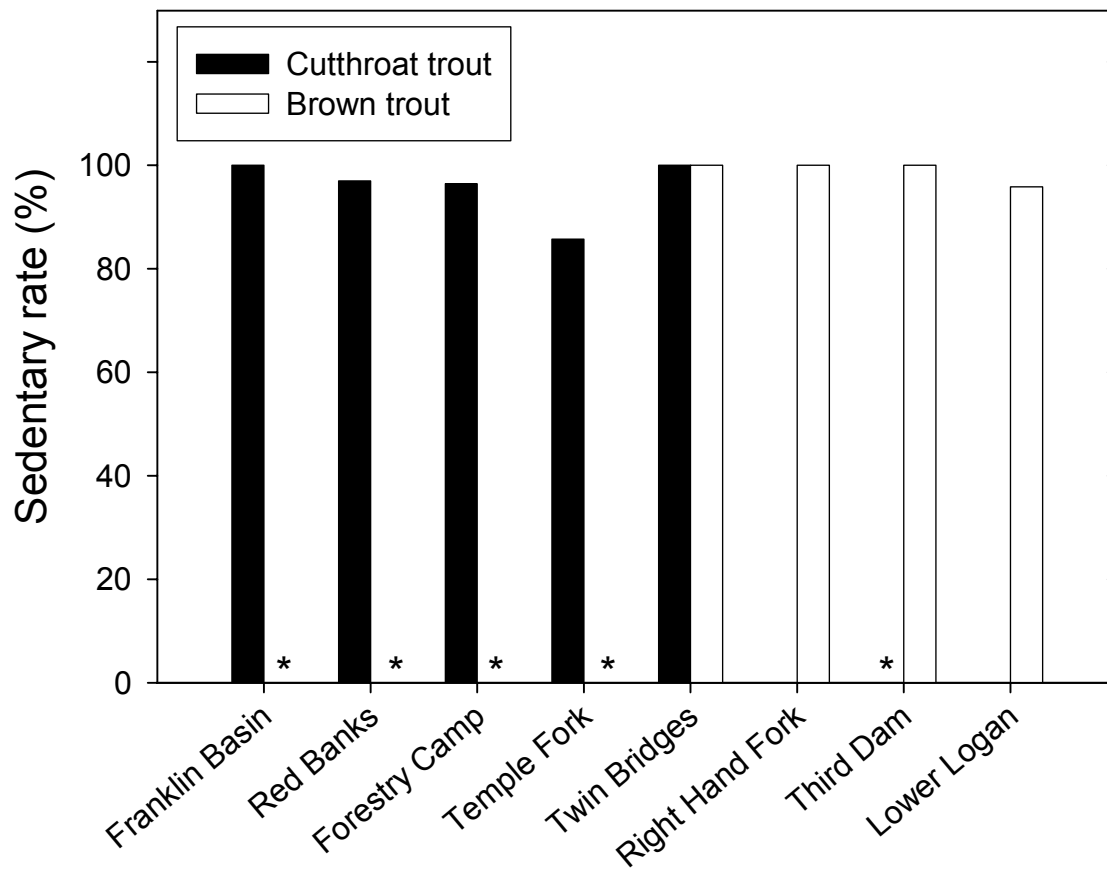


Figure 1.8. Sedentary rates (percentage of recaptured fish that were recaptured at initial tagging site) of cutthroat trout and brown trout in the Logan River, 2003-2004. Asterisks signify that although fish were tagged at the site, none were recaptured. Temple Fork and Right Hand Fork are tributary streams.

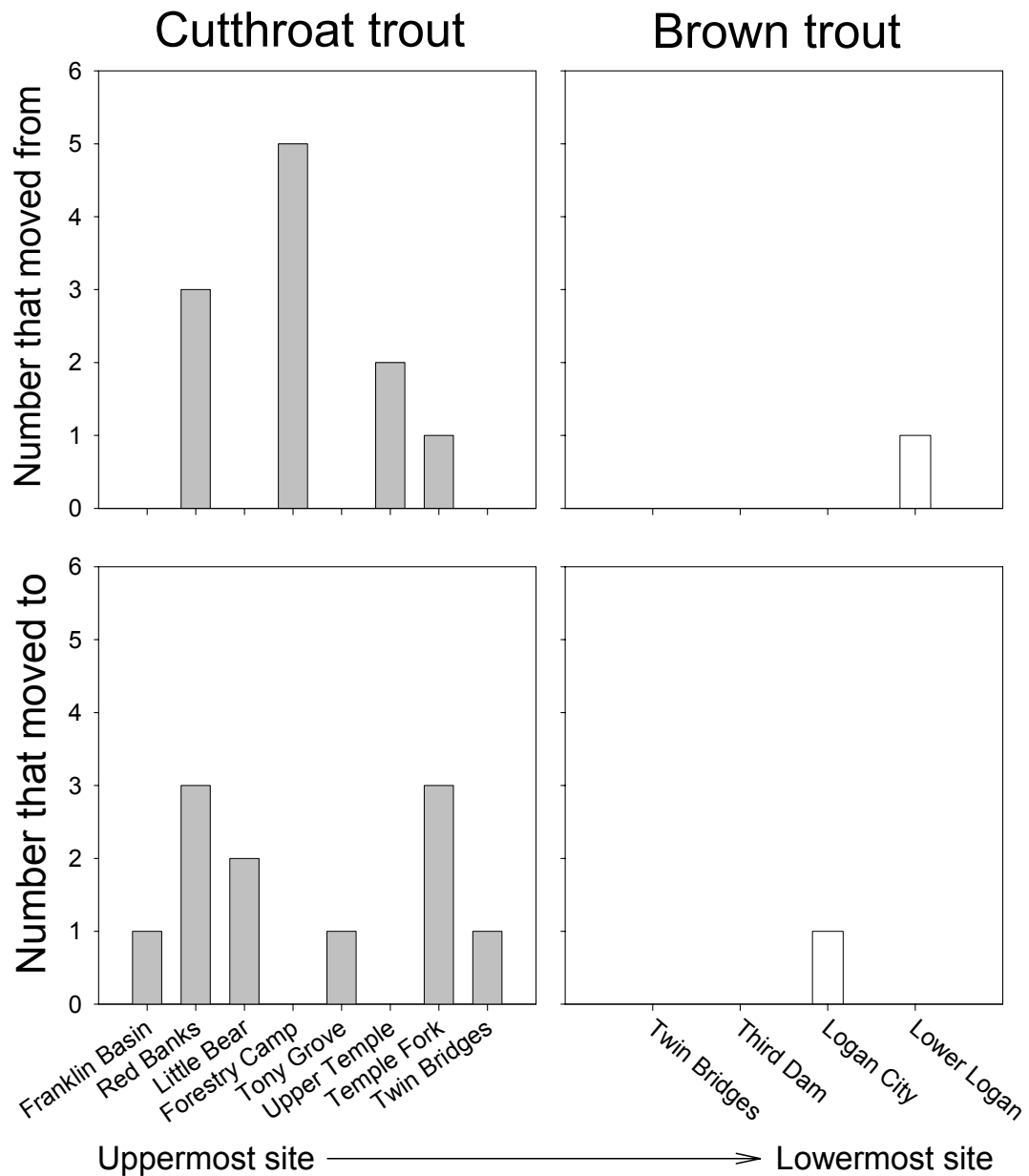


Figure 1.9. Movement of tagged cutthroat trout (left panels) and tagged brown trout (right panels) in the Logan River, 2002 to 2004. Distance from Temple Fork to Red Banks is 9.3 km, while distance from Upper Temple Fork to Temple Fork index site is 630 m (see Table 1.1).

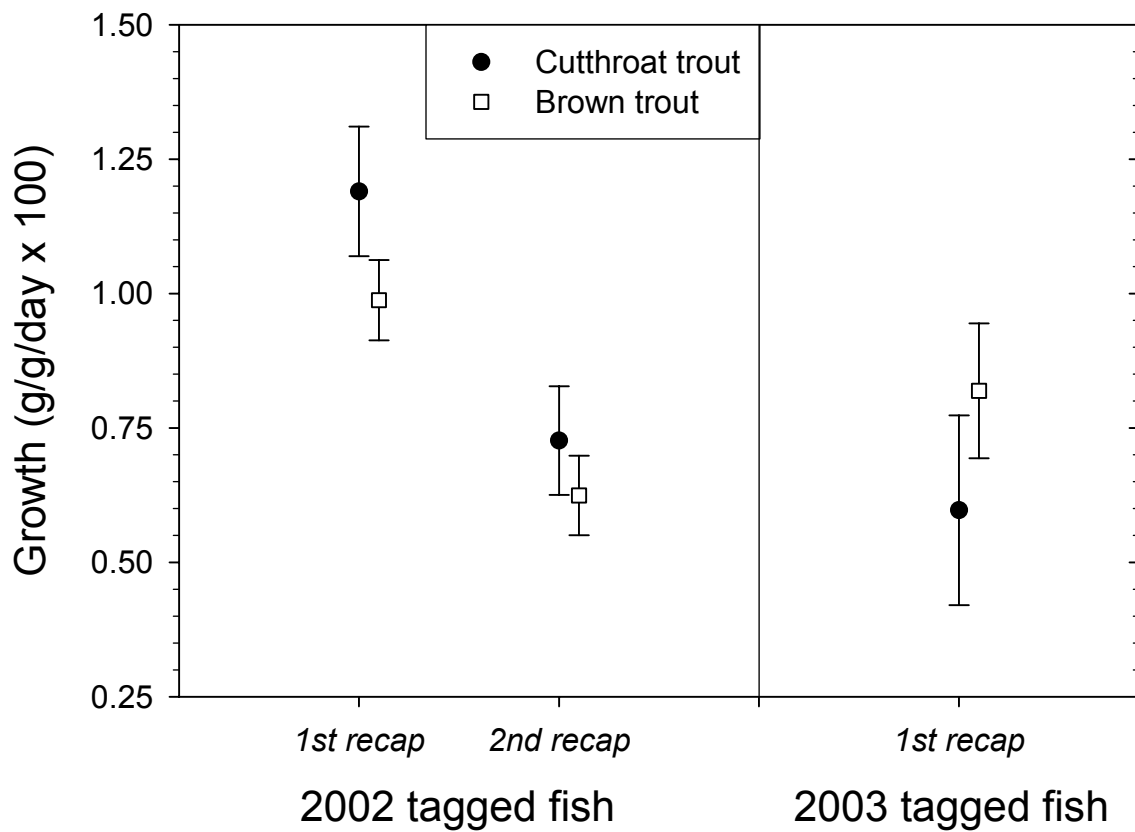


Figure 1.10. Instantaneous growth rates (g/g/day) of tagged and recaptured cutthroat trout and brown trout in the Logan River, 2002-2004: fish initially tagged in 2002 are on the left panel and fish initially tagged in 2003 are on the right panel. Recapture events 1st (after one year) and 2nd (after two years) are noted.

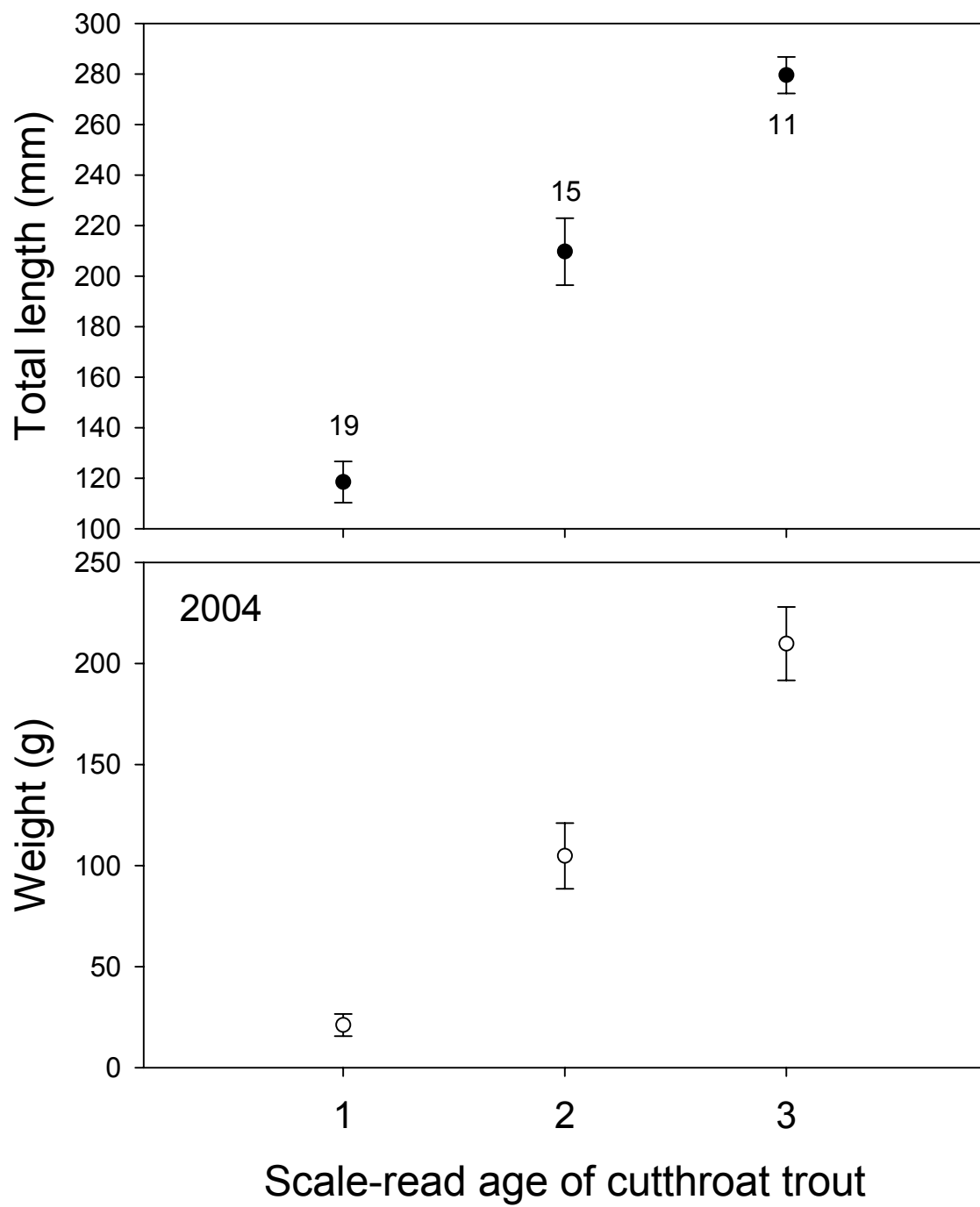


Figure 1.11. Length-at-age and weight-at-age of selected scale-read ages of cutthroat trout from the Logan River, 2004.

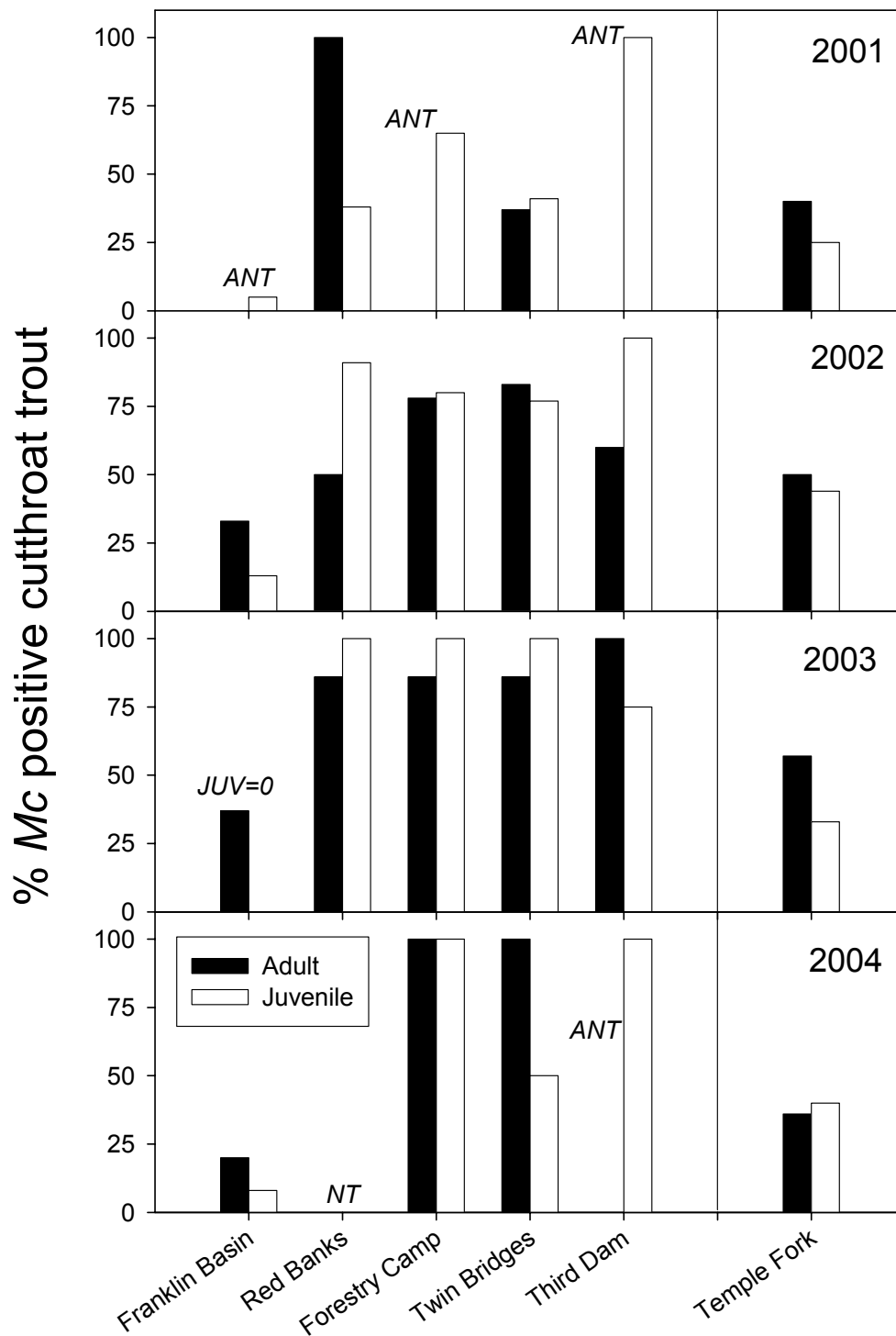


Figure 1.12. Mean percentage of cutthroat trout (all ages combined) by sample site that tested positive for *M. cerebralis* in the Logan River, 2001-2004, based on PCR testing. NS = site not sampled. NC = none captured. NT = samples not tested. ANT = adults not tested.

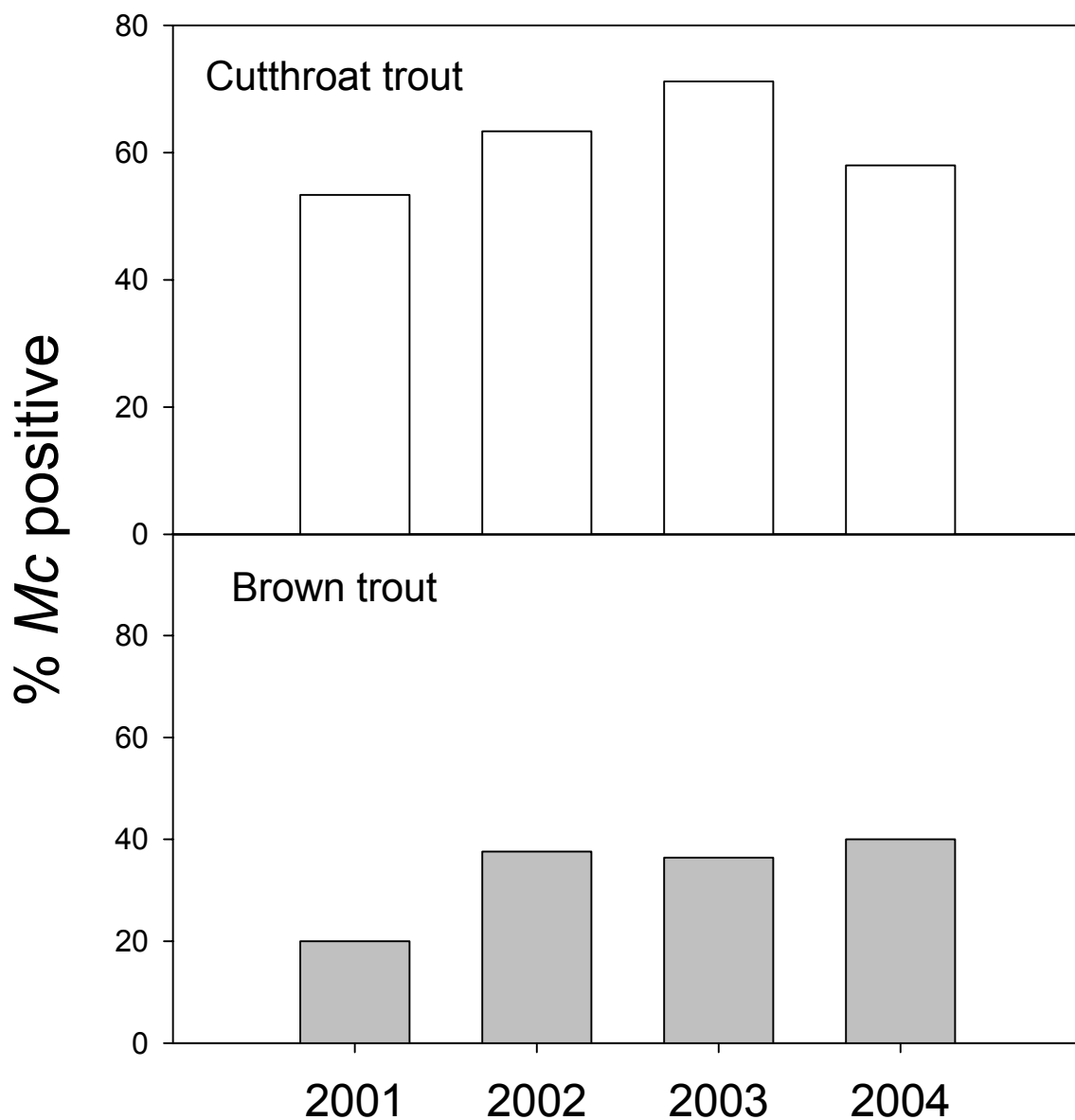


Figure 1.13. Percentage of cutthroat trout and brown trout (all ages and sites combined) that tested positive for *M. cerebralis* in the Logan River and tributaries, over a 4-year period, based on PCR testing.

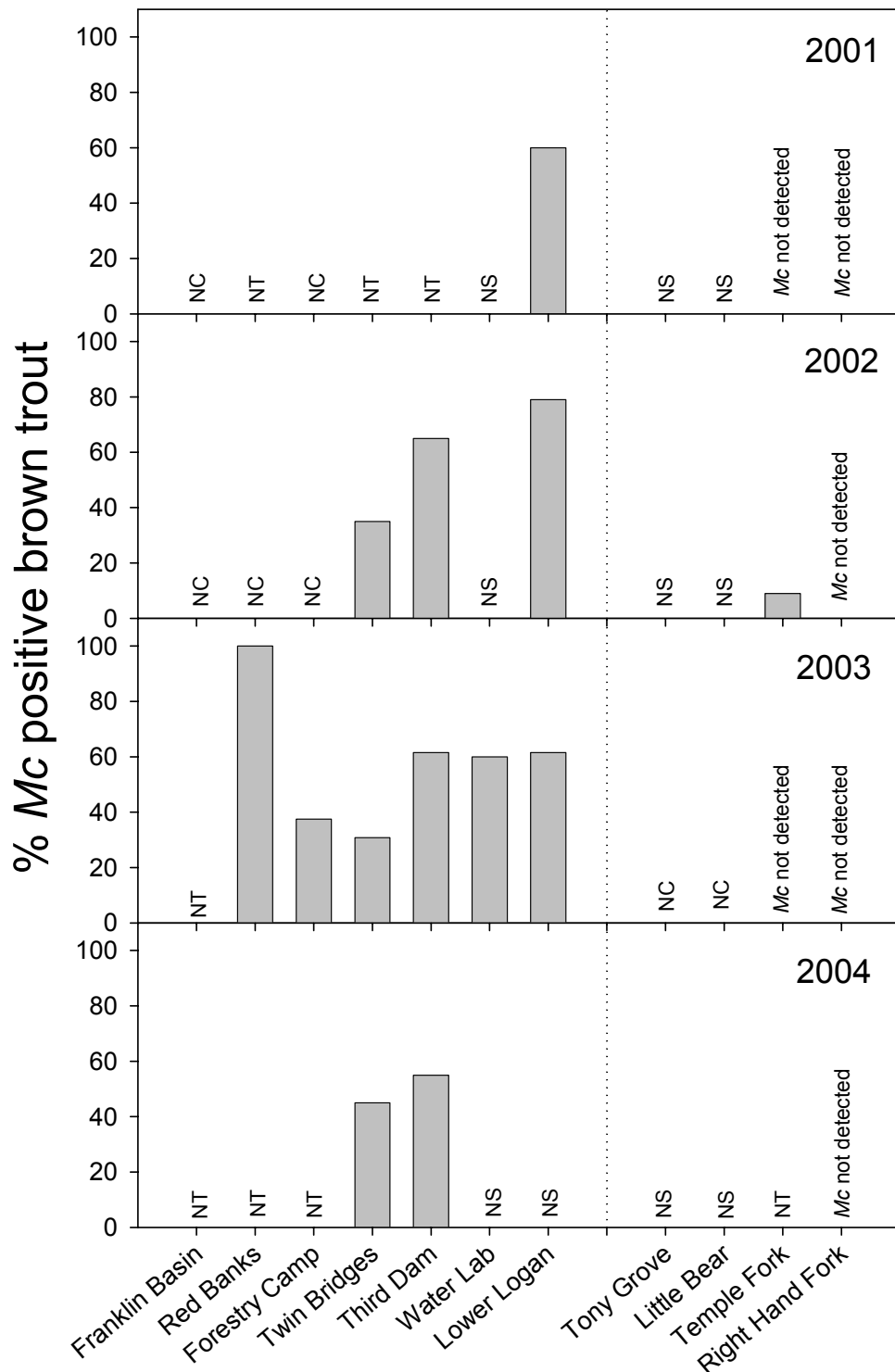


Figure 1.14. Mean percentage of brown trout (all ages combined) by sample site that tested positive for *M. cerebralis* (based on PCR testing) in the Logan River, 2001-2004. NS = site not sampled. NC = none captured. NT = samples not tested.

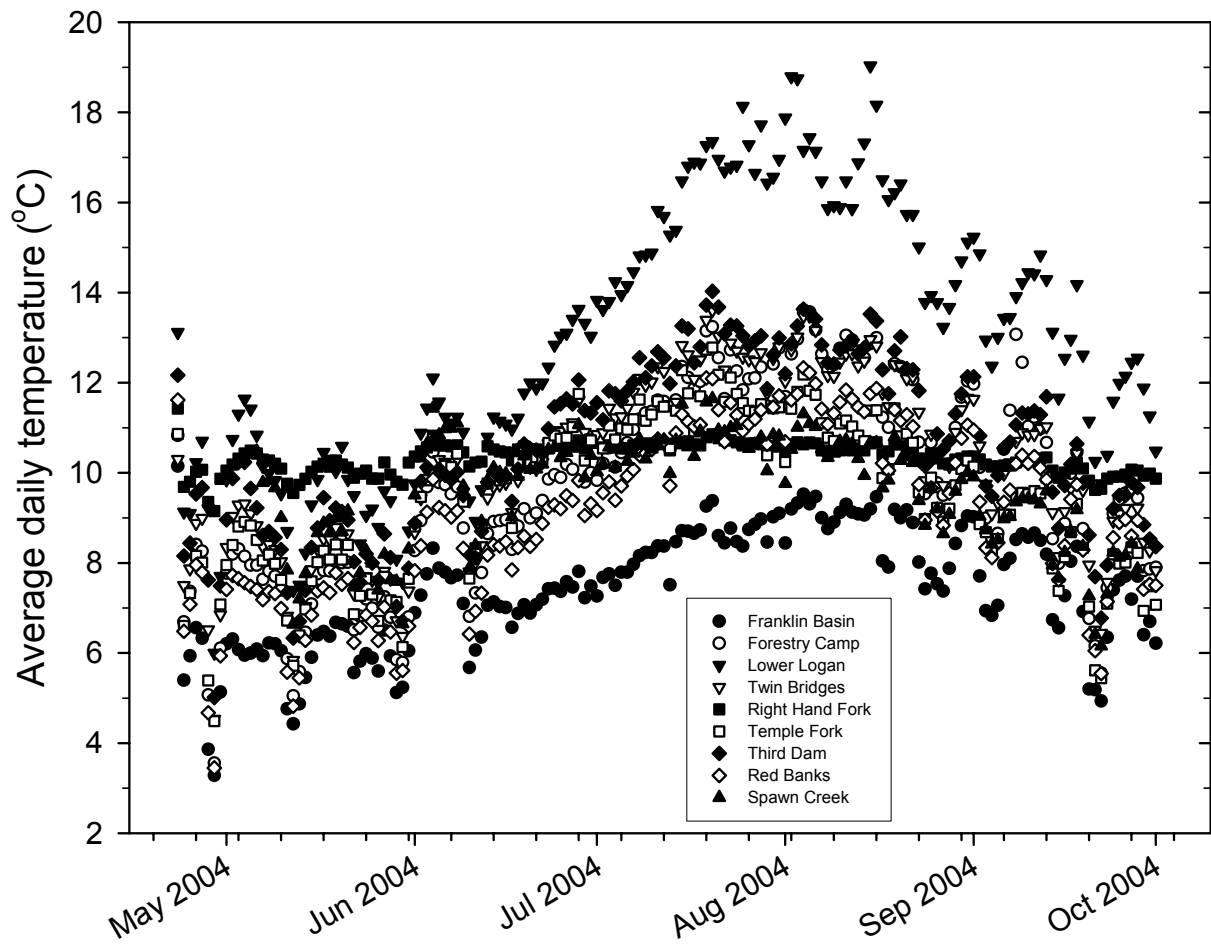


Figure 1.15. Average daily temperatures at six sites along the Logan River and three tributary streams, April-October 2004.

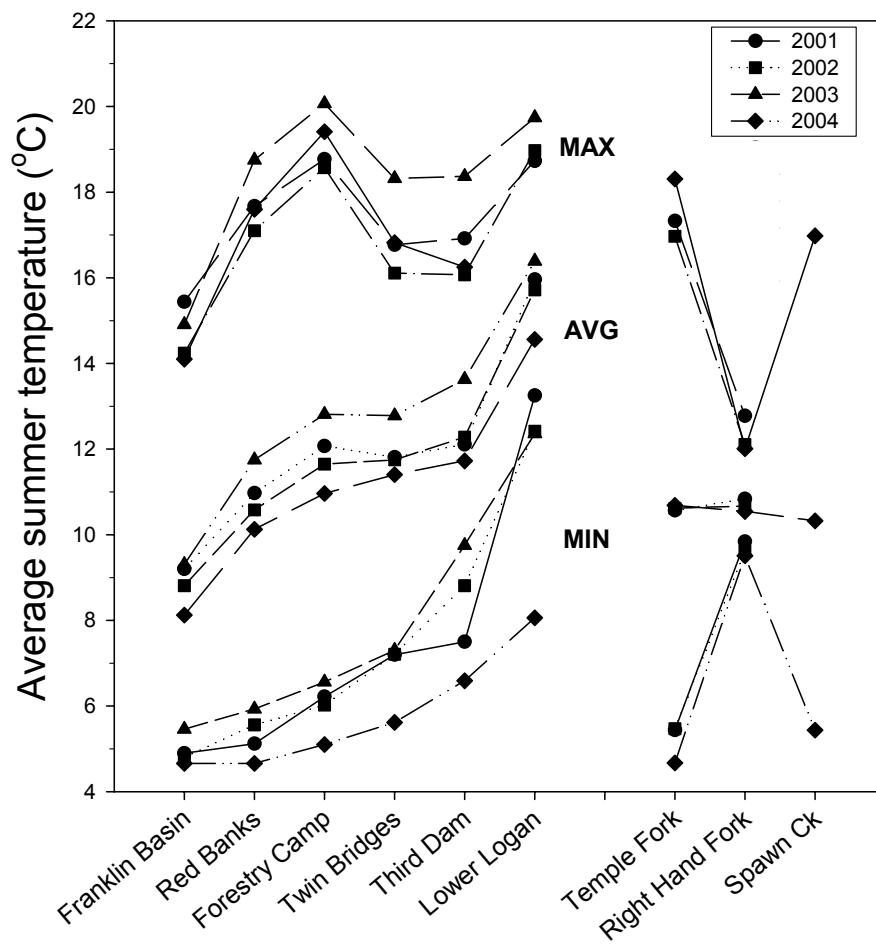


Figure 1.16. Minimum (MIN), average (AVG), and maximum (MAX) summer temperatures at six sample sites along the Logan River and three tributary streams, 2001-2004.

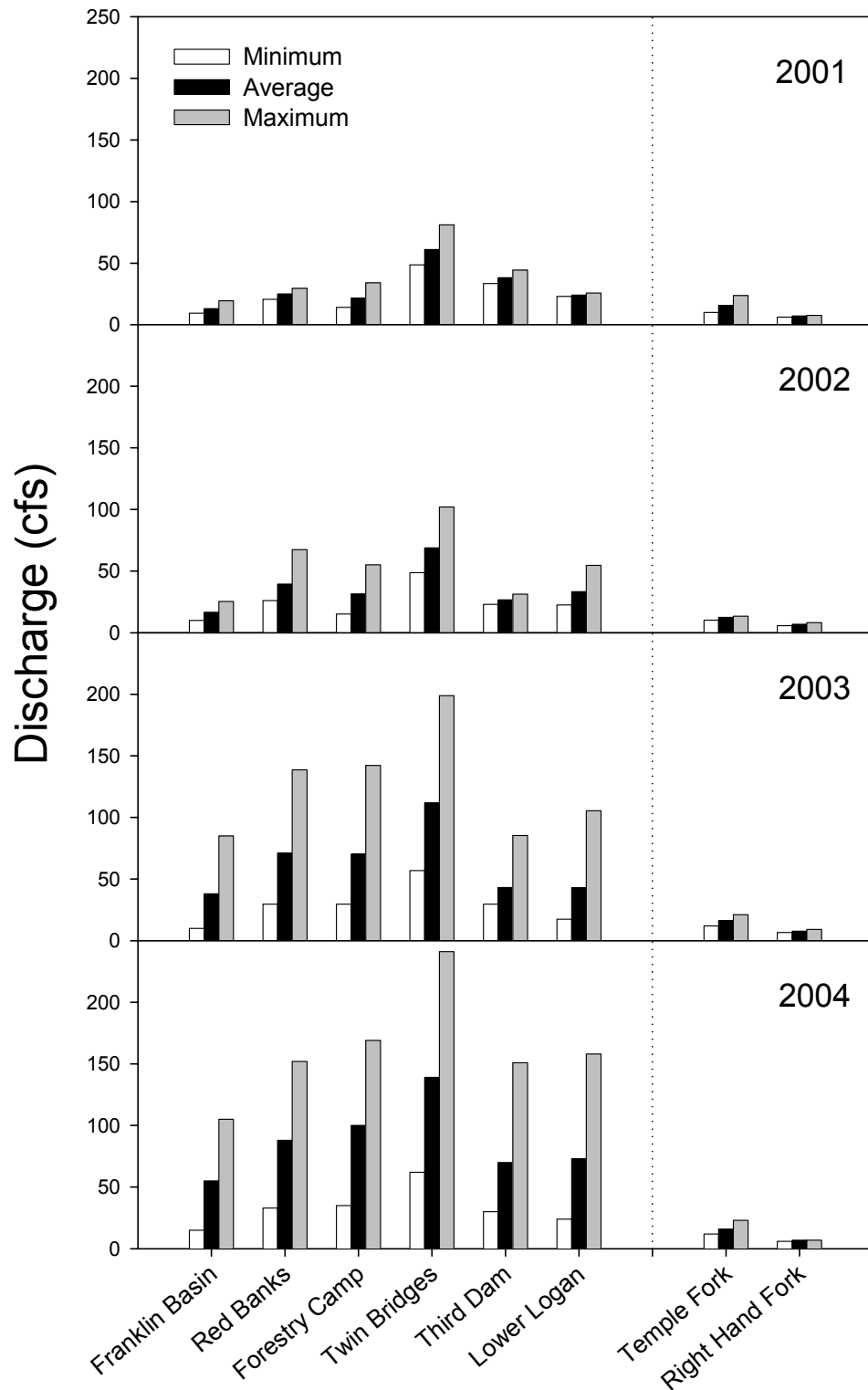


Figure 1.17. Minimum, average, and maximum summer discharge measurements (cfs) at six sites along the Logan River and two tributaries, 2001- 2004.

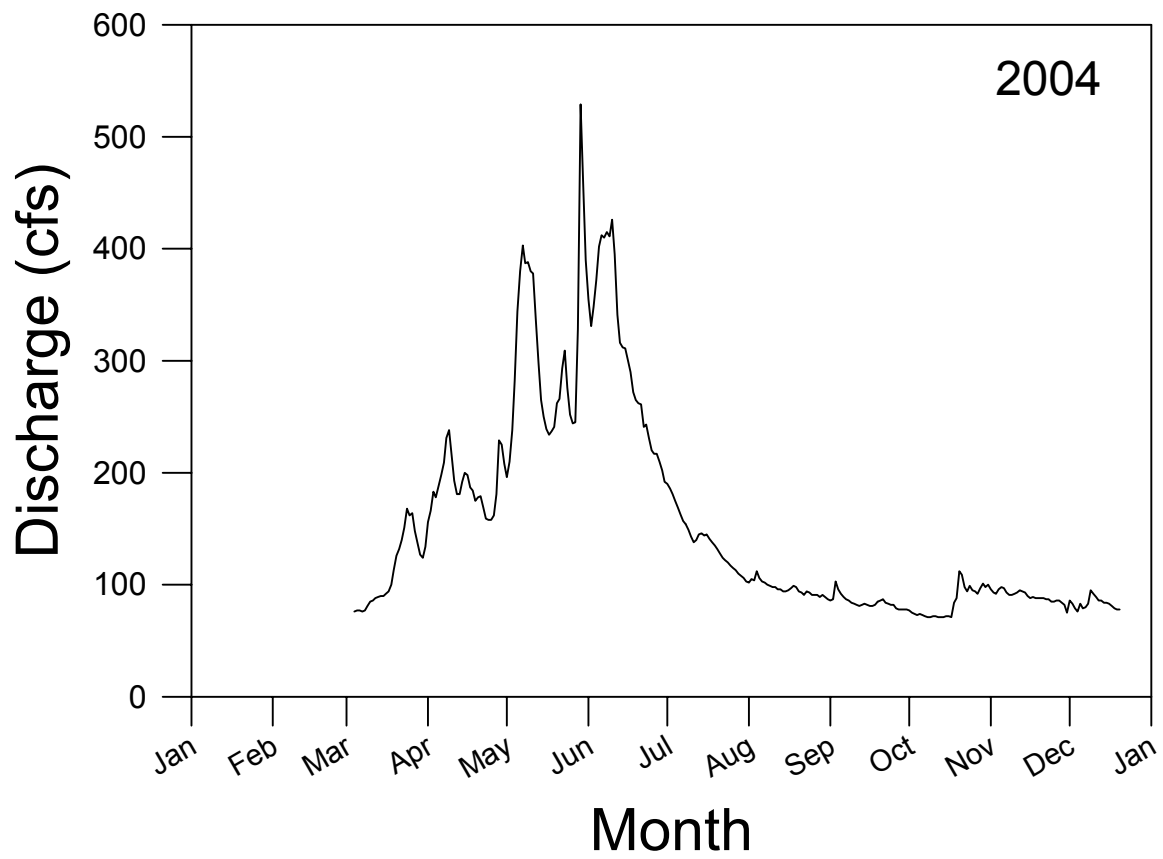


Figure 1.18. Hydrograph for the Logan River, 2004.

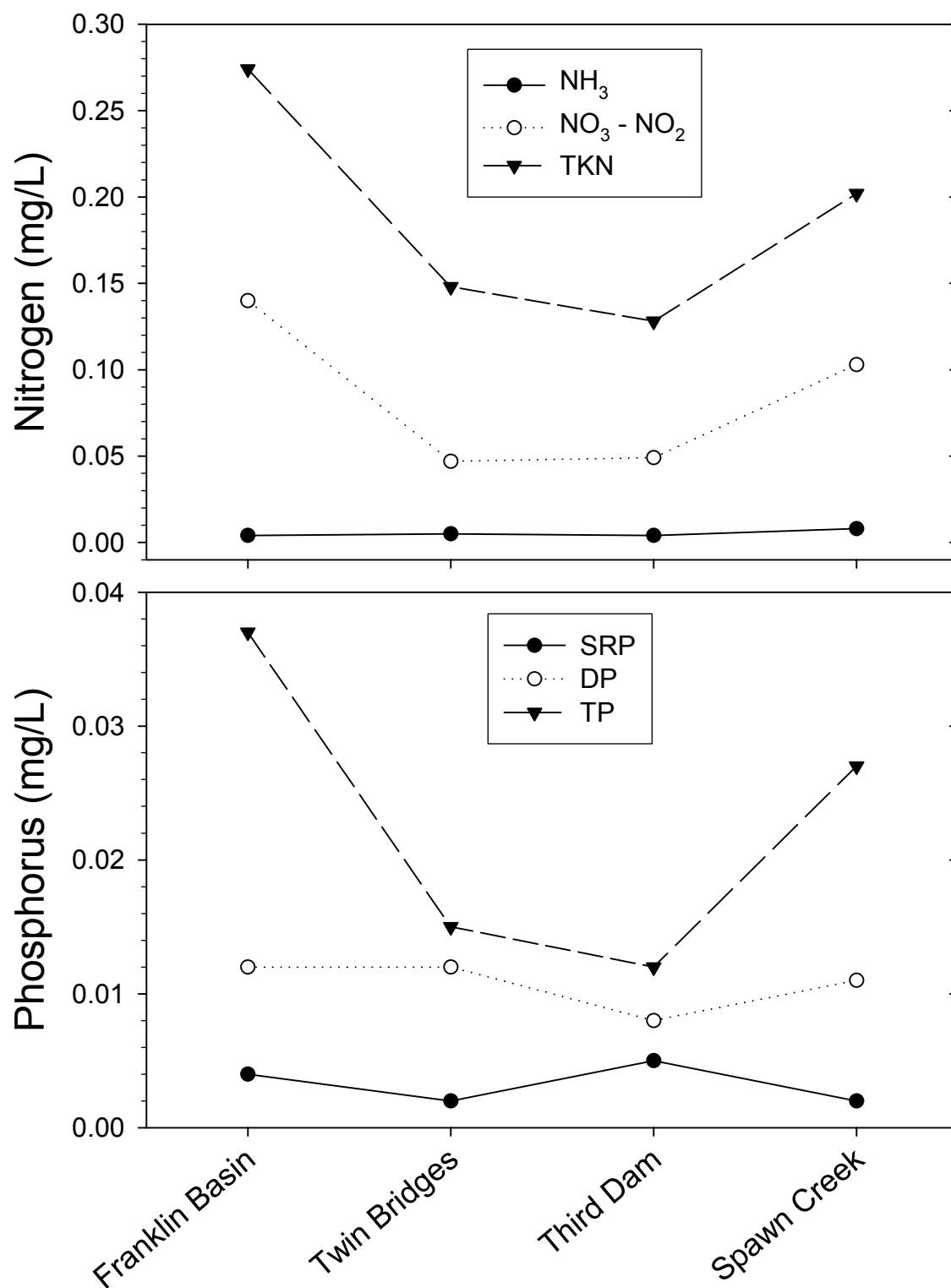


Figure 1.19. Nitrogen and phosphorus concentrations at selected sites in the Logan River drainage, 2004.

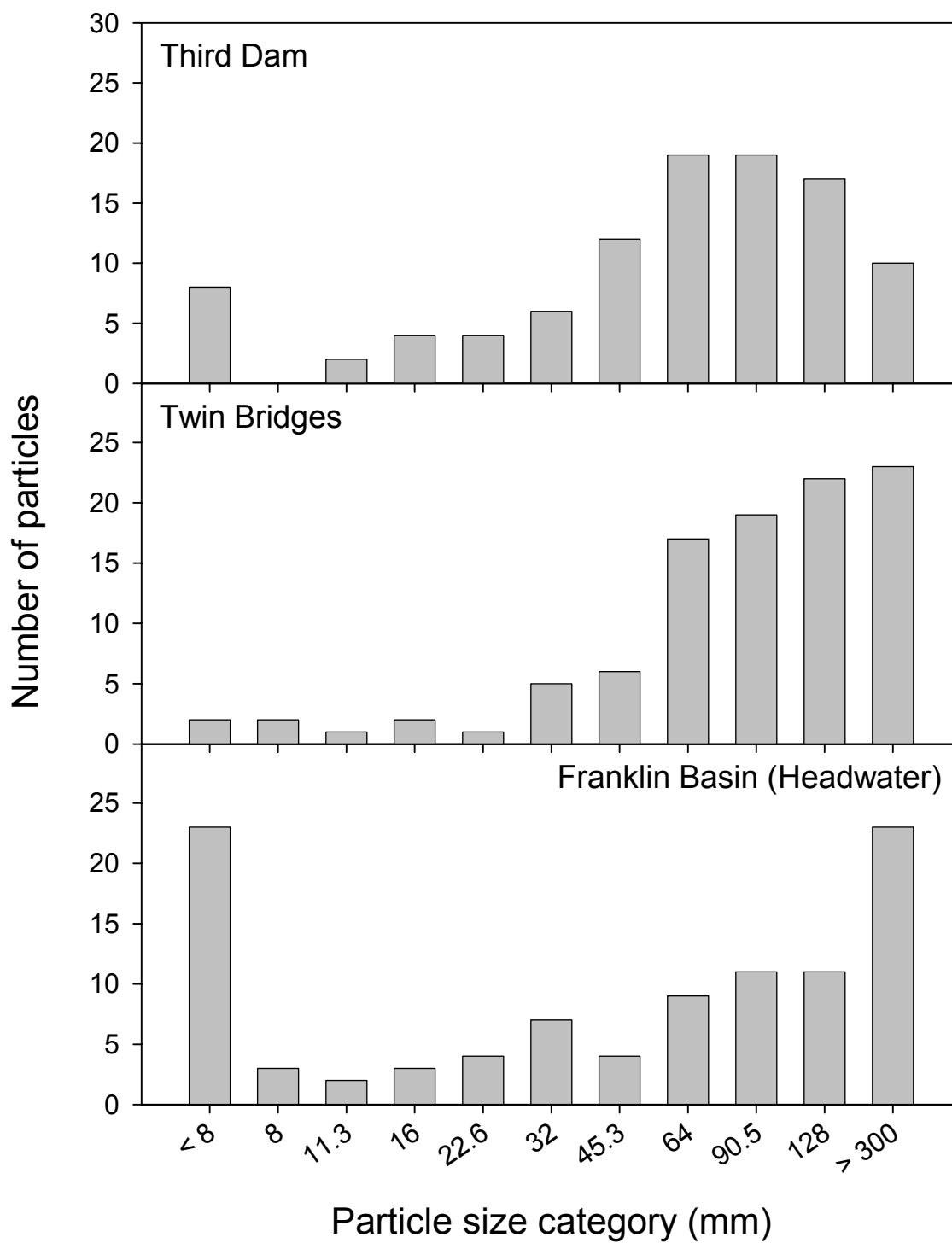


Figure 1.20. Substrate measurements (particle size frequency) at selected sites in the Logan River drainage, 2004.

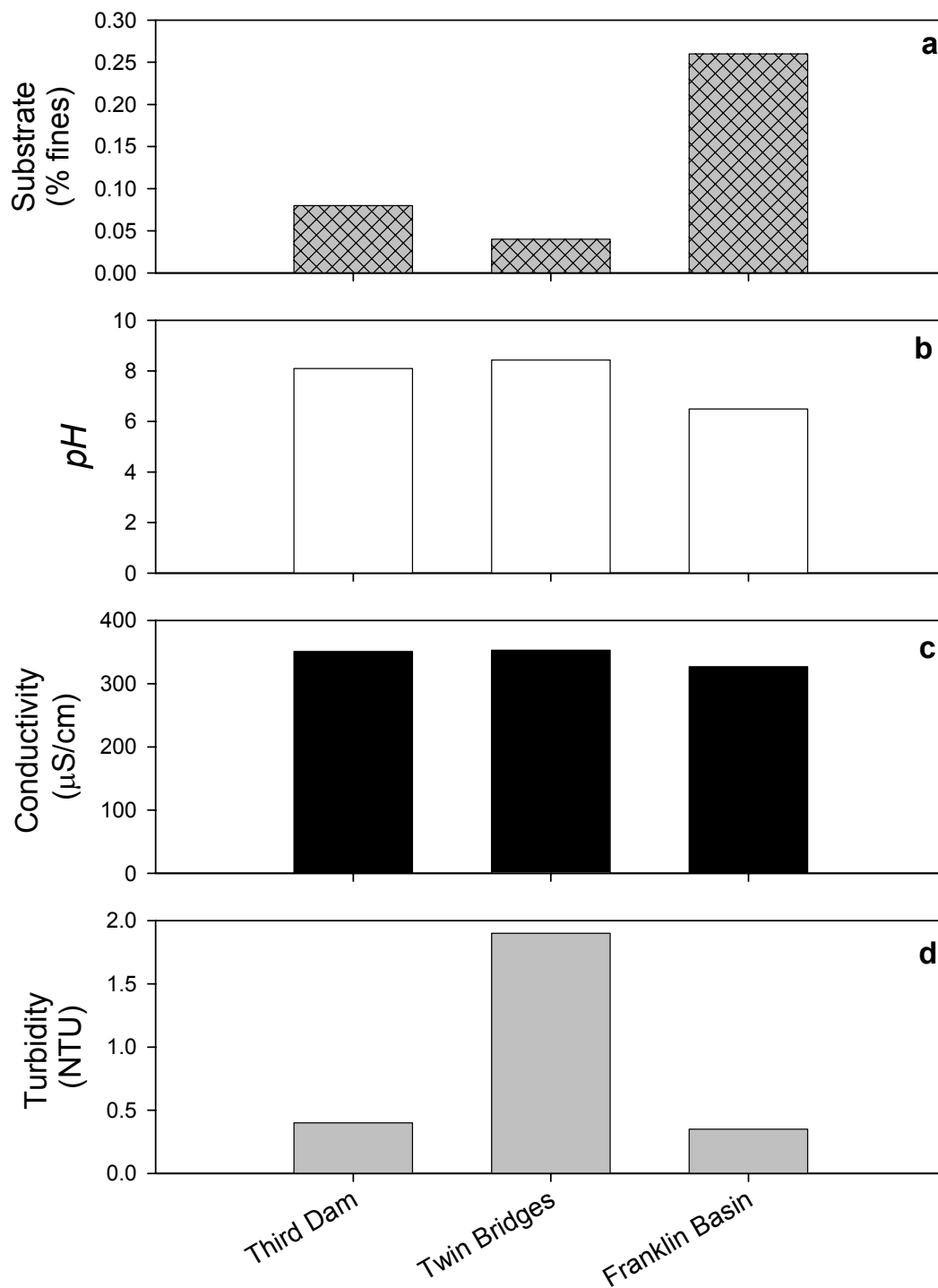


Figure 1.21. Physical variables measured at three sample sites Logan River, 2004: Substrate measured as percent fine sediments (< 10-mm diameter rock particles) on the stream bottom (a), pH (b), conductivity (c), and turbidity (d) of stream water measured at the time fish were sampled.

CHAPTER 2:
**An assessment of the feeding relations between native and
introduced trout in the Logan River: an ontogenetic perspective**

INTRODUCTION

Knowledge of diet and feeding behavior of species inhabiting aquatic systems is critical for effective conservation and management of native fish species in the presence of exotics. For instance, the introduction of opossum shrimp (*Mysis relicta*) into Flathead Lake, Montana, noticeably reduced kokanee salmon (*Oncorhynchus nerka*) abundance through the direct exploitation of zooplankton resources, the primary prey of kokanee (Spencer et al. 1991). Additionally, the introduction of peacock bass (*Cichla ocellarius*) into Gatun Lake, Panama, effectively eliminated six of eight common fish species and drastically reduced a seventh primarily through introductions and predatory impacts (Zaret and Paine 1973). Further, the loss of a weaker species can result from competitive impacts that lead to resource partitioning. This can occur in situations when resources are low and overlap in diet is high (Bohn 2001).

Western species of cutthroat trout (*Oncorhynchus clarki*) are threatened by the predatory and competitive impacts of nonnative species. Brown trout (*Salmo trutta*) were introduced into northern Utah streams in the late 1800s and are presently one of the most abundant trout in the region. Simultaneously, native Bonneville cutthroat trout (*O. c. utah*) have disappeared from 65% of their historic range (UDWR 2001; USFWS 2005), a pattern attributed to the combined affects of habitat degradation and introduced species (Duff 1988). In the Logan River, brown trout occur in high abundance at lower elevations and cutthroat trout occur in high abundance at higher elevations with a zone of very little spatial overlap and low abundance of both species (De la Hoz and Budy 2004). This allopatric species distribution pattern is commonly observed in situations where competition between native and nonnative trout occurs (Fausch 1988, 1989), and/or where predation occurs (Townsend and Crowl 1991).

A recent study on the Logan River provides some experimental evidence for interspecific competition between brown and cutthroat trout; cutthroat trout growth was suppressed in enclosures when they were reared with brown trout versus when reared alone (Chapter 3, *this report*). In contrast, diets (based on isotopic analysis) of wild, in-river cutthroat trout captured in 2003, indicated little dietary overlap and consistent dietary differences between brown and cutthroat trout, demonstrating that competition may not be for food resources (Budy et al. 2004, see *also* Figure A2). However, isotope-based assessment as a long-term descriptor of diet, and feeding

behavior must be validated with diel diet information. Further, consideration of diet changes across life history or ontogeny of these two species is necessary before conclusions about factors like competition can be made (see Vander Zanden et al. 1997).

Energy flow and trophic position can be determined based on both diet and isotopic analysis (Vander Zanden et al. 1997, 1999). Dietary analysis involves point estimate evaluations of the composition and percent contribution of prey to total gut volume or biomass. Stable isotopes, such as nitrogen (^{15}N) and carbon (^{13}C) provide a continuous measure integrating assimilation of energy or mass flow through all the different trophic pathways to an organism (Post 2002). Life stages and life histories can affect the results obtained from sampling stomachs and isotopes.

Table 2.1. The site where fish were collected, the species and age class collected, and whether both species occur together or apart.

| Site | Species present | Occurrence |
|----------------|---|------------|
| Franklin Basin | Cutthroat trout only, juveniles and adults | Allopatry |
| Twin Bridges | Cutthroat and brown trout, juveniles and adults | Sympatry |
| Third Dam | Brown trout only*, juveniles and adults | Allopatry |

* Abundance of cutthroat trout is relatively low.

Most aquatic organisms go through ontogenetic niche shifts during their life cycle in order to minimize mortality and increase growth. Therefore, diet and feeding behavior, and the potential for competition, may differ across life stages. For instance, juveniles tend to feed in areas that are safe from predation; this risk-averse behavior may mean feeding in less productive areas and on different food sources as compared to adults (Brio et al. 2003). Similarly, native cutthroat trout and introduced brown trout go through ontogenetic diet shifts due to life history differences (Mittelbach and Persson 1998). Adult brown trout may have a greater potential for piscivory, and adult cutthroat trout may feed more heavily on terrestrial insects than brown trout, while juveniles of both species consume similar aquatic insects. Thus, there are key uncertainties regarding the diet and feeding behavior of brown and cutthroat trout and how these factors potentially differ across both species life histories. The objective of this project is to provide a better understanding of the diet

and feeding behavior of these two trout species. In this study, we analyzed the diets of adult and juvenile brown trout and cutthroat trout from natural locations where they occur together (in sympatry) and where they occur alone (in allopatry) in the Logan River (Table 2.1).

METHODS

The headwaters of the Logan River are located in the southeastern corner of Idaho, USA. The river enters the northeast corner of Utah at an elevation of 2690 m and runs through Logan Canyon for 64 km to reach the city of Logan, dropping to an elevation of approximately 1371 m (De la Hoz Franco and Budy 2004).

Fish for this research project were collected by electrofishing in August 2004 during the annual fish survey completed as part of a larger study. Three fish collection sites were chosen *a priori* based on the trout species present including: (1) Franklin Basin - a cutthroat trout dominated site where brown trout are virtually non-existent, (2) Twin Bridges - brown trout and cutthroat are equally abundant (sympatry), and (3) Third Dam - a brown trout dominated site where cutthroat trout abundance is negligible. Where possible, at least 30 adults and 15 juveniles of each species were sacrificed using a lethal dose of MS-222. Stomachs were removed by dissection, preserved in 95% ethanol, and diet contents were analyzed in the laboratory. Prey fish in diets were identified to species. Terrestrial and semi-aquatic insects were classified as one group and aquatic invertebrates were identified to order. Prey items were blotted dry and weighed *en masse* based on their classification. Percent composition was calculated based on the weight that the prey item contributed to the total weight of stomach contents as recommended by Bowen (1996).

Diets of brown trout and cutthroat trout were compared using the diet overlap index by Shoener (1970). Diet overlap (D) was calculated as follows:

$$D = 100 \left(1 - 0.5 \times \sum_{i=1}^n |p_{x,i} - p_{y,i}| \right)$$

where $p_{x,i}$ = the proportion of diet category i from stomach of predator x and n = number of prey categories.

In order to evaluate changes in niche breadth with respect to allopatric and sympatric trout distributions, niche width was calculated with Levins index:

$$W = 1 / \left(\sum_{i=1}^n p_i^2 \right)$$

where W = niche width, p_i = proportion of prey category i , and n = the number of prey categories (Levins 1968).

RESULTS

Diet analysis

Both brown trout and cutthroat trout consumed a variety of prey including trichopterans, ephemeropterans, plecopterans, dipterans, hemipterans, coleopterans, mollusks, amphipods, annelids, terrestrial insects (including bees, ants, pill bugs, beetles), sculpin (*Cottus bairdi*), and unidentified insects (pieces of insects that could not be identified as either terrestrial or aquatic). Vegetation and miscellaneous unidentifiable debris were also found in stomachs.

Allopatric cutthroat trout—Ephemeropterans were consumed in the greatest amount by both juveniles (78%) and adults (72%), but in smaller proportions. Additionally, juveniles and adults consumed Trichoptera, Diptera, and terrestrial insects. Other invertebrates (Hemiptera, Coleoptera, Mollusca, Amphipoda, and Annelida) were also consumed by juvenile cutthroat trout (Figure 2.1).

Allopatric brown trout—Trichoptera were consumed in the greatest proportion by both juveniles (41%) and adults (68%). Juveniles consumed Diptera (26%) and other invertebrates (12%) in greater quantities than adults did. Conversely, terrestrial insects were eaten in a greater proportion (50%) by adults, and sculpin (9%) were eaten by the adults, but not by juvenile brown trout (Figure 2.1).

Sympatric cutthroat and brown trout—Where trout species occurred together, both species and age classes ate Trichoptera, Plecoptera, Diptera, and other invertebrates. Ephemeroptera were consumed by juvenile and adult cutthroat trout and juvenile brown trout, but not by adult brown trout (Figure 2.1). Terrestrial insects were eaten by adult cutthroat trout, adult brown trout, and juvenile brown trout. Sculpin were eaten by both adult cutthroat trout and adult brown trout.

Diet overlap

Conspecific juveniles versus adults—Where cutthroat trout occurred alone, diets of juveniles and adults were very similar, with greater than 90% overlap estimated by

Schoener's index. In contrast, diet overlap between juvenile and adult cutthroat trout occurring with brown trout (Twin Bridges) was low (Figure 2.2). Diet overlap between juvenile and adult brown trout was similar whether in sympatry or in allopatry (Figure 2.2).

Sympatric cutthroat and brown trout—Diet overlap between adult cutthroat trout and both adult and juvenile brown trout was very high, nearly 70% overlap in both instances (Figure 2.3). Diet overlap between juvenile cutthroat trout and juvenile and adult brown trout was low, 20% and 27%, respectively (Figure 2.3).

Niche width

Niche width increased as both species and age classes included more prey items in their diets when brown and cutthroat trout occurred together (i.e., in sympatry) versus when they occurred alone (i.e., in allopatry; Figure 2.4). However, niche width for juvenile cutthroat trout remained consistently low whether or not brown trout were present. Adult cutthroat trout and juvenile brown trout had the highest niche widths (4.7) when occurring sympatrically (Twin Bridges site; Figure 2.4).

DISCUSSION

Allopatric adult and juvenile cutthroat trout exhibited very high diet overlap. Diet overlap of over 90% represents identical diets (Krebs 1989), and it is unexceptional that conspecifics would utilize similar prey resources. However, low diet overlap between adult and juvenile cutthroat trout in the presence of brown trout is peculiar. This pattern could result from the fact that adult cutthroat trout greatly expanded their diet breadth when in the presence of brown trout, thereby limiting diet overlap with juvenile cutthroat trout, which demonstrated limited diet plasticity during this study. Further, juvenile cutthroat trout exhibited little diet overlap with adult and juvenile brown trout, and juvenile cutthroat trout niche width breadth did not expand when they occurred with brown trout. The fact that more than 75% of juvenile cutthroat trout diets in the presence of brown trout contained unidentifiable invertebrates, is a confounding factor limiting the strength of the diet data. This could explain in part, the little diet overlap with brown trout and the appearance that juvenile cutthroat trout niche breadth remained narrow.

Diet overlap of juvenile and adult brown trout changed little from allopatry to sympatry, although it was nearly 60%. All age classes of brown trout consumed nearly identical food resources in allopatry and sympatry. Conversely, adult cutthroat trout

demonstrated the greatest increase in niche width from allopatry to sympatry. This suggests that adult cutthroat trout were perhaps forced to consume a wider variety of prey items, including non-preferred prey. This further demonstrates the dietary plasticity of adult cutthroat trout.

Besides competition, these diet shift patterns could result from differences in invertebrate assemblages at sampled sites. However, invertebrate collections in 2001 showed similar assemblages (dominated by ephemeropterans, chironomids, dipterans, and plecopterans; Budy et al. 2002; M. Vinson, *unpublished data*) at each of the sites sampled for diets.

High diet overlap and a great increase in niche width of adult cutthroat trout when they occur in sympatry with brown trout versus when they occur alone (i.e., in allopatry), suggests that brown trout and cutthroat trout may be competing for food resources. A diet overlap greater than 60% can be considered significant, and is suggestive of competition for food resources (Wallace 1981). These results, when coupled with other factors (e.g., distributional pattern, De la Hoz and Budy 2004; growth, condition and movement patterns, Chapters 3 and 4 of this report) indicate that competition is occurring between cutthroat trout and brown trout. Further, the results of this study indicate that juvenile cutthroat trout may be at the greatest risk resulting from competition with brown trout.

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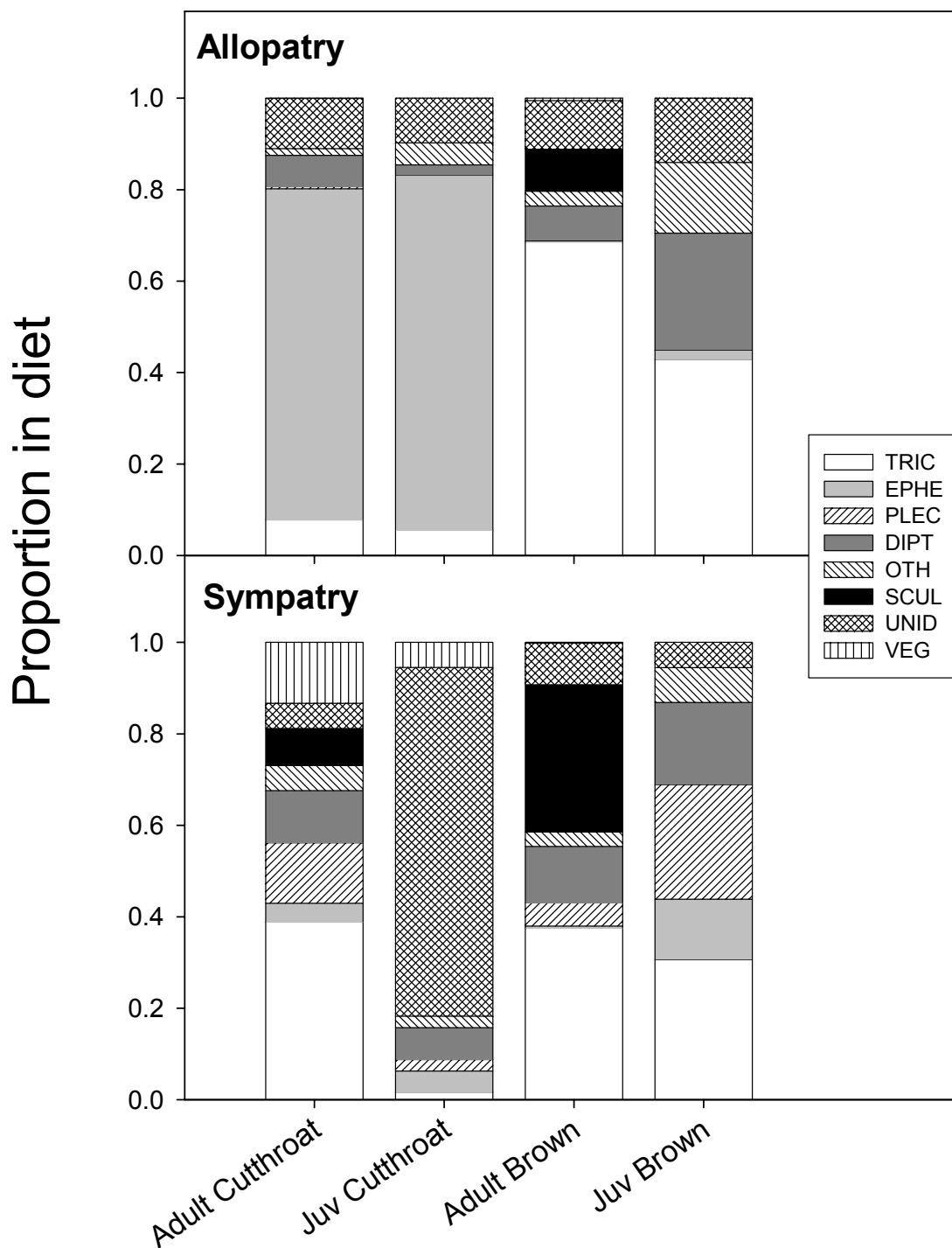


Figure 2.1. Summer diet composition (proportion of diet by wet weight) of juvenile and adult cutthroat trout and brown trout occurring in allopatry (top panel) and sympatry (bottom panel) at three sites in the Logan River, 2004. TRIC = tricopterans; EPHE = ephemeropterans; PLEC = plecopterans; DIPT = dipterans; OTH = other invertebrates including hemipterans, coleopterans, mollusks, amphipods, isopods, annelids, and terrestrial insects; SCUL = sculpin; UNID = unidentifiable invertebrate parts; and VEG = vegetation.

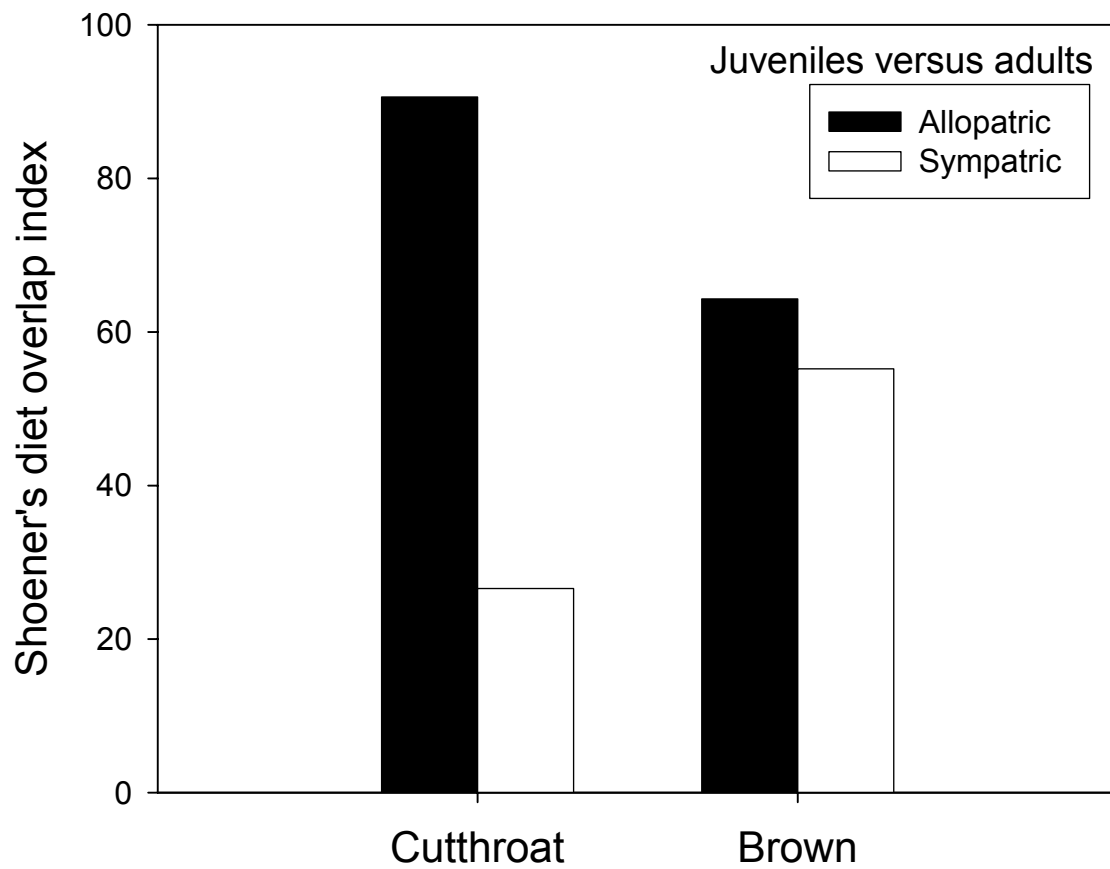


Figure 2.2. Diet overlap (%) of juveniles versus adults for cutthroat trout and brown trout occurring in allopatry and in sympatry in the Logan River, 2004.

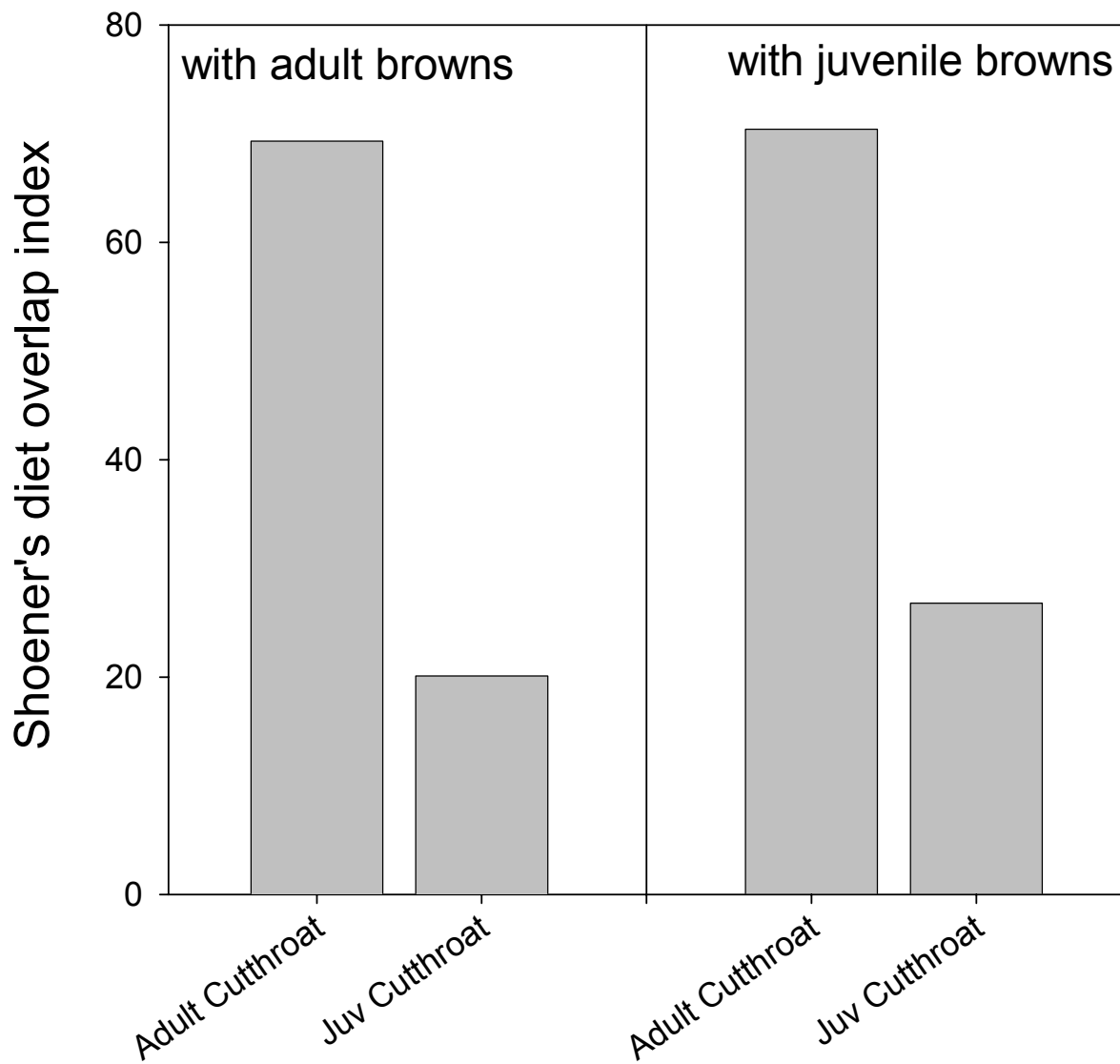


Figure 2.3. Diet overlap (%) of juvenile and adult cutthroat trout occurring with adult brown trout and juvenile brown trout at the Twin Bridges site on the Logan River, 2004.

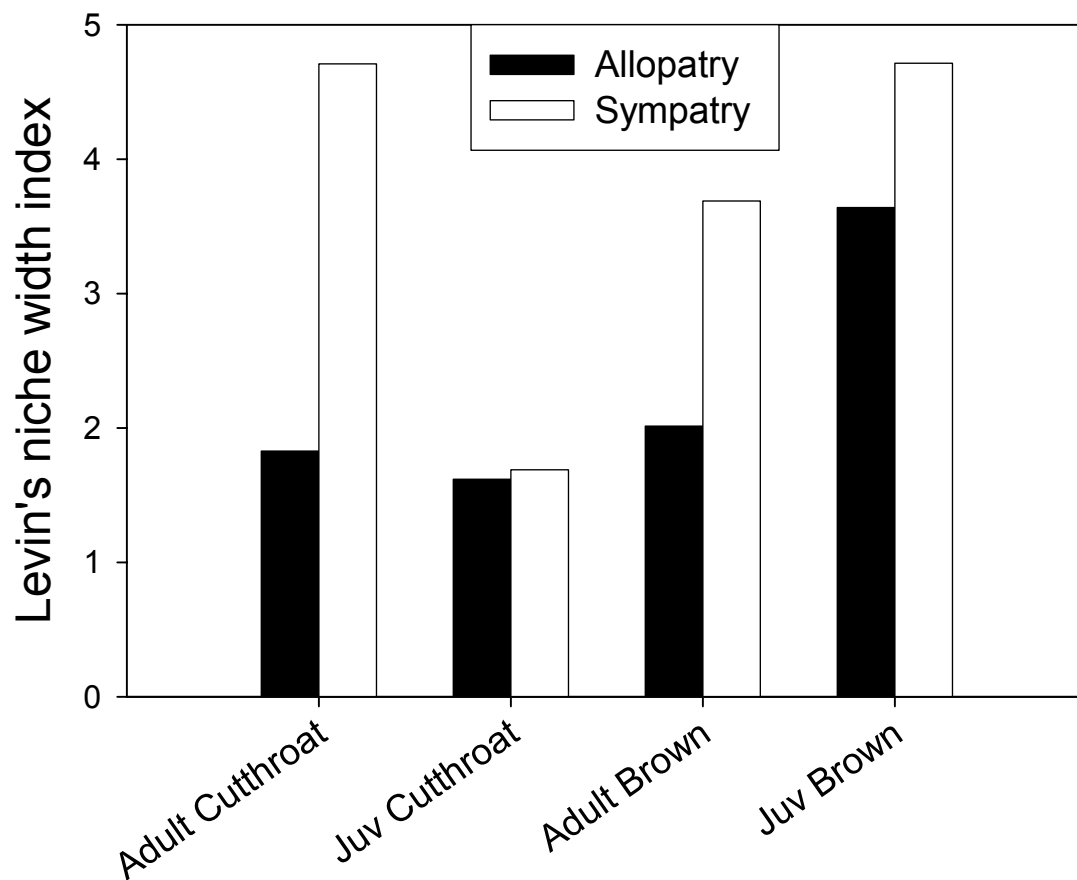


Figure 2.4. Niche width of juvenile and adult cutthroat trout and brown trout when occurring in allopatry and in sympatry in the Logan River, 2004.

CHAPTER 3:

Competitive and thermal effects on brown trout and cutthroat trout performance along an altitudinal gradient: an experimental evaluation

INTRODUCTION

Patterns of fish-species replacement along altitudinal gradients commonly occur in montane rivers and streams throughout the world (Taniguchi and Nakano 2000). This phenomenon – termed ‘altitudinal species zonation’ because of the distinct species zones observed along upstream and downstream gradients – occurs in response to factors operating differentially across elevations. Zonation may be due to the response of individual species to the availability of suitable habitat conditions that vary with elevation (e.g., temperature; Vincent and Miller 1969; Rahel and Hubert 1991; Bozek and Hubert 1992). For instance, each species may have a different thermal physiology and thus exhibit a distribution pattern reflecting the spatial arrangement of suitable temperatures within a river network (Magoulick and Wilzbach 1998a).

More locally, species-zonation patterns can be the result of an interaction between abiotic and biotic factors (Dunson and Travis 1991; Fausch et al. 1994). For example, temperature-mediated competition may be the reason why salmonid species segregate along altitudinal gradients (Fausch 1989; Fausch et al. 1994; De la Hoz Franco and Budy 2004). Under this scenario, high-elevation species are hypothesized to be superior competitors at cold temperatures and to exclude low-elevation species from areas dominated by those conditions, while the reverse is thought to be true at low-elevation, warmer sites. In the absence of the competitor(s), all species may be physiologically capable of living at all sites (Taniguchi and Nakano 2000). While there have been several recent experiments designed to evaluate temperature-mediated competition as an explanation for salmonid zonation (See Table 3.5 in Discussion for a review of these studies), results have been variable (DeStaso and Rahel 1994; Novinger 2000).

Because of the threatened and endangered status of many native fishes, it is imperative to understand the influence of temperature-mediated competition on salmonid zonation in streams. Nonnative trout invasions are perceived as one of the greatest threats to native salmonid diversity in North America (Dunham et al. 2002; Quist and Hubert 2004). In many watersheds of the western U.S. and Canada, native cutthroat trout (*Oncorhynchus clarki* subspecies) persist only in headwater reaches while nonnative brook (*Salvelinus fontinalis*) and exotic brown trout (*Salmo trutta*)

replace them at lower elevations (Fausch 1989; De la Hoz Franco and Budy 2004). Given the imperiled status of cutthroat trout (Gresswell 1988; Behnke 1992; Young 1995), identifying the causes of zonation in native–nonnative trout systems is of considerable importance. Specifically, understanding whether cutthroat trout distributional limits are set by abiotic conditions, competition with exotic species, or an interaction between the two will lead to different strategies when attempting to increase the size and spatial extent of cutthroat trout populations – a goal common of recovery plans (e.g., Lentsch et al. 1997).

In this study, we evaluated the causes of spatial segregation between exotic brown trout and native Bonneville cutthroat trout (*O. c. utah*) in a northern Utah, U.S.A. stream. Native to the ancient Lake Bonneville Basin of the Intermountain U.S., Bonneville cutthroat trout are only present in a fraction of their historic range (35%; USFWS 2001; UDWR 2005) and have been considered for U.S. Endangered Species Act protection (Duff 1988; Young 1995; Lentsch et al. 1997). In contrast, brown trout (a species native to Europe) are widely distributed in the region and abundant in many streams that were historically dominated by cutthroat trout. When they co-occur, brown trout and cutthroat trout segregate along altitudinal gradients (De la Hoz Franco and Budy 2004). To understand this pattern, we experimentally assessed the interacting roles of interspecific competition and water temperature on brown and cutthroat trout performance in a field setting.

STUDY SITE

We conducted our experiment within a 45-km segment of the Logan River, (41°44'N, 111°46'W), a stream that originates in the Bear River Mountain Range of northern Utah and drains into the terminal Great Salt Lake system (Figure 3.1). This mountain stream of moderate elevation (study reach range: 1503 - 2091 m) and gradient (0.015 m·m⁻¹) flows through a broad valley in its upper reaches and a deeply dissected canyon in its lower reaches. The climate of the area is characterized by cold, snowy winters (January air temperature: low, -9 °C; high, 0 °C; mean precipitation 4.0 cm) and hot, dry summers (July air temperature: low, 15 °C; high, 31 °C; mean precipitation 1.6 cm), yielding a hydrograph dominated by a spring-snowmelt flood (554 cfs) followed by base-flow conditions (~ 100 cfs).

In addition to Bonneville cutthroat trout, the species of primary interest in our study, other native fishes present in the Logan River include mottled sculpin (*Cottus bairdi*) and mountain whitefish (*Prosopium williamsoni*). Introduced species include brown trout, with rainbow (*Oncorhynchus mykiss*) and brook trout also present but in low numbers. Species abundance varies with elevation in the Logan River, producing

three fish zones (De la Hoz Franco and Budy 2004): 1) a low-elevation brown trout dominated zone; 2) a high-elevation cutthroat trout dominated zone; and 3) a mid-elevation transitional area (Figure 3.2).

METHODS

Experimental design

We evaluated the influence of competition and temperature on brown trout–cutthroat trout zonation through an enclosure experiment where these species were reared together (i.e., in sympatry) and alone (i.e., in allopatry) at six points systematically spaced along the thermal gradient present in the Logan River. The spatial aspect of our design thus incorporates the natural temperature range and the three fish zones of the Logan River, allowing us to simultaneously assess the role of temperature and competitive interactions in zonation. We did this using a substitutive competition experiment (*sensu* Fausch 1998) within the context of a randomized complete block design. At each site, we constructed three 20-m² (6.0 m X 3.3 m) enclosures using steel T-posts and 13-mm black plastic mesh; within each site, we randomly assigned treatments to enclosures. The treatment levels were: 1) eight cutthroat trout in allopatry, 2) eight brown trout in allopatry, and 3) four brown and four cutthroat trout in sympatry; the density of experimental fish in enclosures (0.40 fish·m⁻²) reflects the upper limit of densities observed for trout in the Logan River (Budy et al. 2004).

Trout used in the experiment were collected from allopatric locations within the study watershed (brown trout from Right Hand Fork; cutthroat trout from Beaver Creek and the Logan River at Franklin Basin; Figure 3.1) using backpack electrofishing methods. Brown (mean TL: 180 mm [95% CI: 175-185]) and cutthroat trout (mean TL: 173 mm [95% CI: 167-178]) used in our experiment were of similar starting total length (TL); however, due to the natural size structure present in the Logan River, experimental brown trout were slightly longer than experimental cutthroat trout. Upon collection, we transported all fish to laboratory raceways and held them at 10°C for an 8-d acclimation period to ensure that all fish had the same recent thermal history prior to exposure to experimental temperatures. During this period, fish were starved, weighed, measured, and given a uniquely numbered T-bar anchor tag.

Individual fish were randomly assigned to each site-treatment combination and introduced into enclosures on 14 July 2003 to begin a 42-d trial. During this period, fish were assumed to have sufficient prey resources (e.g., terrestrial, benthic, and/or drifting macroinvertebrates); a pilot study indicated that when enclosure mesh was

cleaned of debris, invertebrate drift was unimpeded (Table 3.1). We cleaned all enclosures at least once every 48 hours during the trial period to provide a regular supply of prey. Other than routine cleaning visits, we allowed fish to interact with minimal disturbance during the experiment. On 25 August 2003 the experiment was concluded, and all fish were collected from enclosures (using electrofishing and underwater collection methods), weighed, and measured. As a rule, we included in our analysis only those enclosures that contained at least five of the eight experimental fish and at least two of each species (for sympatric replicates only). For both species, this resulted in five and six replicates for sympatric and allopatric treatment groups, respectively.

Table 3.1. Comparison of drift density and invertebrate size between drift samples taken directly upstream (outside enclosure) and immediately downstream (inside enclosure) of the front of an enclosure constructed of 13-mm plastic mesh. Values represent the mean (95% CI) from three replicate 30-minute drift samples taken at dusk using 10-cm diameter drift nets. Inside and outside samples were taken on separate and successive evenings.

| | Drift density (number·m ⁻³) | Invertebrate size (mm) |
|-------------------|--|---------------------------|
| Outside enclosure | 21 (16 - 25) | 2.6 (2.5 - 2.7) |
| Inside enclosure | 30 (17 - 42) | 2.5 (2.2 - 2.8) |

Fish performance

We initially evaluated the performance of brown and cutthroat trout using instantaneous growth, G , where

$$G = [(\ln W_{final} - \ln W_{initial}) \cdot t^{-1}] \cdot 100 \quad (1)$$

and W is the weight (mass) in grams and t is trial length in days. Due to high tag loss (25%) and the disappearance of some fish, however, we were unable to assess growth for all individuals in all enclosures. Rather than lose information on the performance of unidentified fish, we used a condition index that could be computed for every individual (i.e., regardless of identity) as a surrogate for growth in our analysis. We evaluated condition using the relative weight index, W_r , where

$$W_r = W/W_s \cdot 100 \quad (2)$$

W is the observed weight of a given fish, and W_s is its predicted weight (g) based on its measured total length (mm) and a 'standard' length-weight relationship for the species. Our standard length-weight relationships were those estimated for wild, Logan River brown and cutthroat trout sampled during annual monitoring activities (brown trout, $W_s = 1.708 \cdot 10^{-5} TL^{2.905}$; cutthroat trout $W_s = 6.193 \cdot 10^{-5} TL^{2.670}$; Budy et al. 2004). There was a consistent positive relationship between W_r and G for experimental fish that retained tags (least squares regression results: brown trout, $F_{1,58} = 24.9$, $P < 0.0001$, $R^2 = 0.30$; cutthroat trout, $F_{1,47} = 17.3$, $P = 0.0001$, $R^2 = 0.27$), rendering condition a reasonable surrogate for growth in our study.

We summarized the distribution of individual-level performance within enclosures for both species, separately, using two measures. First, to assess the performance of the 'average' fish we computed the median condition value (W_r -med.) for a given site-treatment combination. As a second, potentially more sensitive indicator of competition, we computed the maximum condition value (W_r -max.) for all members of a species in each enclosure. We did this because dominant individuals can monopolize the most profitable foraging sites and obtain the greatest condition value in a competitive environment (e.g., Nakano 1995; Sloman et al. 2000). Finally, pre-trial condition values (W_r -med. and W_r -max.) were similar for fish assigned to the two treatment groups for both species (multivariate analysis of variance using Wilks' lambda: brown trout, $F_{2,8} = 1.5$, $P = 0.269$; cutthroat trout, $F_{2,8} = 0.6$, $P = 0.551$) indicating that any differences observed at the end of the trial are due to experimental effects.

Environmental variable measurement

To evaluate the effects of environmental factors on performance and competitive relationships, and to account for cage effects in our analysis, we quantified several habitat characteristics at both the site and enclosure levels. Water temperature, the site-level (block) variable of primary interest in our study, was measured hourly using data loggers. From these data, we computed the average daily mean, minimum, and maximum temperature for the 42-d period. We also quantified stream size at the site level using a single base-flow discharge measurement made with an electromagnetic flow meter.

In addition to taking site-level environmental measurements, we assessed habitat within individual enclosures. First, we measured the size distribution of streambed particles using a Wolman pebble count (Wolman 1954), which was summarized by the median particle size (D50). To account for fine sediment deposition caused by

velocity differences between the inside and outside of enclosures and due to changes in flow across the 42-day period, we estimated the percent of the enclosed area covered by fines (< 8 mm) visually at the beginning and end of the trial. We also measured depth (cm) and velocity ($\text{cm}\cdot\text{s}^{-1}$) at 20 evenly spaced points within a grid spanning each enclosure. Finally, we quantified an index of invertebrate abundance based on the assumption that the area upstream of each enclosure was the main source of drifting prey during the experimental period. We collected three benthic invertebrate samples approximately 2 m upstream of each enclosure using a 0.09-m^2 Surber sampler. We preserved samples in 95% ethanol and transported them to the laboratory, where all invertebrates were identified to the level of order using a dissecting microscope. We measured the body length of up to 30 individuals in each order and estimated average dry biomass using order-level length-mass regressions (Benke et al. 1999). We computed the average density ($\text{number}\cdot\text{m}^{-2}$) and dry biomass ($\text{mg}\cdot\text{m}^{-2}$) of invertebrates in the orders Ephemeroptera, Plecoptera, Diptera, and Trichoptera – the chief prey items of brown and cutthroat trout (De la Hoz Franco and Budy 2004).

Statistical analysis

Our analysis occurred in two phases. First, we compared the upstream–downstream temperature profile measured during our experiment to a literature-based descriptor of the thermal physiology of each species, without any consideration of trial results. Thus, we contrasted minimum, mean, and maximum water temperatures from the six sites with the thermal growth optima of brown trout ($13 - 18\text{ }^{\circ}\text{C}$; Elliot and Hurley 2000; Ojanguren et al. 2001) and cutthroat trout ($13 - 19\text{ }^{\circ}\text{C}$; based on the optimum growth temperature-lethal temperature relationship of Jobling [1981] and published thermal physiology data for Bonneville cutthroat trout [Wagner et al. 2001; Johnstone et al. 2003]).

For the second phase of our analysis, we compared condition between treatment groups within each species as a function of temperature through a sequential, three-step process. First, we evaluated the effects of treatment (i.e., evidence for competition), temperature (i.e., evidence for a thermal control on performance), and a treatment-by-temperature interaction (i.e., evidence for temperature-mediated competition) on median and maximum condition simultaneously using multivariate analysis of covariance (MANCOVA). Second, we tested the influence of the same model effects on each response separately using analysis of covariance (ANCOVA) in a *post-hoc* context. Third, when the temperature-by-treatment interaction was significant in a given *post-hoc* model, we contrasted ANCOVA-adjusted means at a low and high temperature level. For temperature effects, we were primarily interested

in understanding how temperature extremes affect the outcome of competition; thus, we used two temperature metrics (average daily minimum and maximum) each in a separate analysis sequences. All analyses were completed using PROC GLM in SAS (SAS Institute 2002). Due to the low replication and high variability of our dataset, we assessed significance using $\alpha = 0.10$ for MANCOVA-based tests and a Bonferroni-adjusted α -level otherwise (i.e., $\alpha = 0.10/2 = 0.05$ for *post-hoc* ANCOVA tests and $\alpha = 0.05/2 = 0.025$ for least-squares means comparisons).

Finally, during the preliminary phase of analyzing our dataset we found clear evidence of an enclosure effect (on condition) related to site-level differences in stream size. Enclosures at high flow sites experienced greater sediment deposition and had reduced invertebrate abundance relative to low flow sites; consequently, brown and cutthroat trout median (brown trout: $R_{\text{allo}} = -0.62$, $R_{\text{sym}} = -0.81$; cutthroat trout: $R_{\text{allo}} = -0.69$, $R_{\text{sym}} = -0.79$) and maximum condition (brown trout: $R_{\text{allo}} = -0.95$, $R_{\text{sym}} = -0.56$; cutthroat trout: $R_{\text{allo}} = -0.96$, $R_{\text{sym}} = -0.53$) values were strongly and negatively related to discharge in both treatment groups. In order to account for this variation and enhance our power to detect temperature and treatment effects, if present, we included stream size as an equal-slope covariate (i.e., fit without interactions) in all models.

RESULTS

Longitudinal temperature profile

In general, water temperatures measured during the experiment decreased with increasing elevation across the study reach (Figure 3.3; Table 3.2). Mean and maximum temperatures increased across the three upper-most sites (Franklin Basin to Tony Grove) and then remained relatively constant in the downstream direction; minimum temperature increased as a nearly linear, inverse function of elevation. The greatest diel fluctuation (maximum – minimum temperature) was observed at a mid-elevation site (Tony Grove). Finally, based on published information on the thermal physiology of brown and cutthroat trout (see Methods), it appears that both species experienced optimum growth temperatures during part of every day at all but the uppermost site (Franklin Basin).

Experimental effects of temperature and competition on trout

On average, seven of the eight experimental fish were recaptured in enclosures. One replicate (i.e., a site-treatment combination) had to be withheld from analysis (Twin

Bridges-sympatric) because of fish losses (n = 3 remained). We witnessed and surmised that fish losses were primarily due to predation by birds.

We observed positive growth among those fish that could be identified definitively (i.e., retained tags). Overall, brown trout and cutthroat trout growth averaged $0.833\% \cdot d^{-1}$ (range: 0.056 to $2.386\% \cdot d^{-1}$) and $0.318\% \cdot d^{-1}$ (range: -0.412 to $1.512\% \cdot d^{-1}$), respectively. Brown trout weight was similar to that of non-experimental Logan River fish of the same size, with an overall mean relative weight (condition) of 100.2% (range: $79.7 - 119.1\%$). Cutthroat trout weighed less than the standard weight equation predicted, attaining a mean condition value of 83.7% (range: $63.5 - 106.0\%$). Brown trout median and maximum condition was higher in sympatric (mean ± 2 SE: W_r -med., $106.5 \pm 5.2\%$; W_r -max., $112.2 \pm 4.9\%$) compared to allopatric enclosures (mean ± 2 SE: W_r -med., $98.5 \pm 2.9\%$; W_r -max., $106.9 \pm 5.4\%$). Thus, brown trout performance was independent of cutthroat trout presence. In contrast, cutthroat trout condition was reduced in sympatry relative to allopatry; this difference was greater for maximum (mean ± 2 SE: sympatric, $84.9 \pm 3.7\%$; allopatric, $96.2 \pm 6.1\%$) than median condition (mean ± 2 SE: sympatric, $82.4 \pm 5.0\%$; allopatric, $85.6 \pm 3.6\%$). These results thus demonstrate an asymmetric, negative competitive effect of brown trout on cutthroat trout.

Our statistical assessment of experimental effects illustrates three important results. First, the effect of site-level differences in discharge on condition was ubiquitous among models evaluated for the two species (Tables 3.3 and 3.4). Thus, a non-temperature covariate (discharge) helped us account for a large proportion of variability in the response. Second, both MANCOVA and post-hoc ANCOVA results indicate that neither cutthroat trout presence, water temperature, nor their interaction had a demonstrable effect on brown trout condition (Table 3.3; Figure 3.4). This constitutes a lack of statistical support for a competitive effect – temperature-mediated or otherwise – of cutthroat trout on brown trout. For cutthroat trout, treatment and/or temperature-by-treatment interaction effects were significant in all but the minimum temperature-median condition model (Table 3.4), indicating that brown trout had a negative competitive impact on cutthroat trout condition (Figure 3.4). At a maximum temperature of 12°C , allopatric cutthroat trout attained a maximum condition value nearly 20% greater than did cutthroat trout reared with brown trout (W_r -max. least-squares means comparison: $t = 6.3$, $df = 6$, $P = 0.001$). Allopatric cutthroat trout outperformed their sympatric conspecifics at a maximum temperature of 17°C as well ($t = 2.5$, $df = 6$, $P = 0.047$), but the difference (6.5%) was not significant (i.e., after adjusting the ANCOVA α -level [0.05] for two post-hoc means comparisons). Cutthroat trout median condition differed between treatment groups as a function of

Table 3.2. Site-level and enclosure-level habitat attributes of 2003 experimental enclosures. 'BNT' = brown trout, 'CUT' = cutthroat trout, and a '-' indicates that that value applies to all enclosures at that particular site.

| Site | Treatment | Site-level attributes | | | | | Enclosure-level attributes | | | | | | |
|----------------|-----------|-----------------------|----------------|----------------|----------------|--------------------|----------------------------|-----------------------------------|-----------------------|---------------------|-------------|---|--|
| | | Elevation (m) | Mean T (°C) | Min. T (°C) | Max. T (°C) | Discharge (cfs) | Depth (cm) | Velocity (cm·s ⁻¹) | Start Fines (%) | End Fines (%) | D50 (mm) | Prey Density (no.·m ⁻²) | Prey Biomass (mg·m ⁻²) |
| Lower Canyon | CUT | 1,503 | 13.9 | 11.8 | 16.2 | 32 | 33 | 18 | 6 | 45 | 34 | 418 | 5,056 |
| | BNT | - | - | - | - | - | 32 | 32 | 0 | 3 | 90 | 1,056 | 12,444 |
| | BNT+CUT | - | - | - | - | - | 29 | 25 | 0 | 3 | 60 | 1,184 | 12,778 |
| Chokecherry | CUT | 1,564 | 12.5 | 10.4 | 14.8 | 95 | 41 | 16 | 56 | 79 | 12 | 292 | 3,489 |
| | BNT | - | - | - | - | - | 34 | 23 | 33 | 74 | 4 | 262 | 3,178 |
| | BNT+CUT | - | - | - | - | - | 33 | 25 | 0 | 43 | 45 | 318 | 3,800 |
| Twin Bridges | CUT | 1,715 | 13.1 | 10.1 | 16.0 | 70 | 44 | 17 | 50 | 88 | 4 | 316 | 2,978 |
| | BNT | - | - | - | - | - | 33 | 21 | 22 | 73 | 4 | 470 | 3,600 |
| | BNT+CUT | - | - | - | - | - | 28 | 20 | 22 | 45 | 12 | 631 | 5,033 |
| Tony Grove | CUT | 1,891 | 12.9 | 8.9 | 17.5 | 36 | 26 | 22 | 0 | 45 | 50 | 286 | 4,367 |
| | BNT | - | - | - | - | - | 36 | 8 | 22 | 58 | 25 | 167 | 2,100 |
| | BNT+CUT | - | - | - | - | - | 31 | 21 | 11 | 33 | 62 | 256 | 3,389 |
| Red Banks | CUT | 1,970 | 9.9 | 6.9 | 13.8 | 37 | 42 | 32 | 0 | 5 | 112 | 1,177 | 7,200 |
| | BNT | - | - | - | - | - | 30 | 29 | 0 | 30 | 45 | 662 | 4,722 |
| | BNT+CUT | - | - | - | - | - | 34 | 36 | 6 | 5 | 85 | 746 | 6,756 |
| Franklin Basin | CUT | 2,091 | 8.1 | 6.1 | 11.2 | 16 | 44 | 22 | 0 | 35 | 95 | 379 | 5,133 |
| | BNT | - | - | - | - | - | 27 | 17 | 0 | 28 | 75 | 436 | 5,833 |
| | BNT+CUT | - | - | - | - | - | 26 | 21 | 13 | 42 | 21 | 303 | 3,889 |

Table 3.3. Brown trout ANCOVA results, by temperature metric (minimum, T_{min} ; maximum, T_{max}) and response variable (median and maximum condition). Bold-faced effect names with a double asterisk are significant ($\alpha = 0.10$) based on MANCOVA results (Wilks' λ). Bold-faced F -statistics and P -values denote effect significant ($\alpha = 0.05$) in *post-hoc* ANCOVA models. Note: the model effect 'Site' is the covariate discharge.

| Temperature Model | Effects | Median Condition | | | Maximum Condition | | |
|-------------------|----------------------|------------------|------------|--------------|-------------------|-------------|--------------|
| | | R^2 | $F_{1,6}$ | P -value | R^2 | $F_{1,6}$ | P -value |
| Minimum | Treatment | 0.76 | 1.7 | 0.243 | 0.77 | 0.7 | 0.431 |
| | Site** | | 4.1 | 0.090 | | 11.4 | 0.015 |
| | T_{min} | | 0.3 | 0.611 | | 0.4 | 0.568 |
| | T_{min} *Treatment | | 0.3 | 0.577 | | 1.7 | 0.241 |
| Maximum | Treatment | 0.77 | 1.9 | 0.220 | 0.73 | 0.1 | 0.798 |
| | Site** | | 6.4 | 0.045 | | 8.8 | 0.025 |
| | T_{max} | | 0.0 | 0.851 | | 0.6 | 0.463 |
| | T_{max} *Treatment | | 0.8 | 0.392 | | 0.3 | 0.626 |

maximum temperature in a similar fashion (Figure 3.4); however, the interaction effect in this case was only marginally significant ($F_{1,6} = 5.7$, $P = 0.054$; Table 3.4). In sum, brown trout greatly reduced cutthroat trout condition at all but the warmest of temperatures observed in our experiment. Experimental brown trout condition, in contrast, was generally unresponsive to temperature and/or competition with cutthroat trout.

DISCUSSION

A central tenet of stream ecology is that abiotic conditions and biological communities change predictably along longitudinal (upstream–downstream) gradients (Vannote et al. 1991). This is particularly true for salmonids in stream environments, where species segregate into discrete 'zones' and water temperatures change over relatively short distances (Vincent and Miller 1969). Such systems are thus ideal for assessing the interacting roles of biotic interactions and abiotic factors in determining species distributions. Accordingly, we evaluated the potentially interacting roles of interspecific

competition and temperature on the performance of two trout species in an effort to understand the causes of salmonid zonation.

Table 3.4. Cutthroat trout ANCOVA results, by temperature metric (minimum, T_{min} ; maximum, T_{max}) and response variable (median and maximum condition). Bold-faced effect names with a double asterisk are significant ($\alpha = 0.10$) based on MANCOVA results (Wilks' λ). Bold-faced F -statistics and P -values denote effect significant ($\alpha = 0.05$) in *post-hoc* ANCOVA models. Note: the model effect 'Site' is the covariate discharge.

| Temperature Model | Effects | Median Condition | | | Maximum Condition | | |
|-------------------|---|------------------|-------------|--------------|-------------------|-------------|--------------|
| | | R^2 | $F_{1,6}$ | P -value | R^2 | $F_{1,6}$ | P -value |
| Minimum | Treatment | 0.65 | 1.0 | 0.359 | 0.88 | 8.4 | 0.028 |
| | Site** | | 7.7 | 0.032 | | 14.6 | 0.009 |
| | T_{min} | | 0.4 | 0.562 | | 0.7 | 0.437 |
| | T_{min} *Treatment | | 0.4 | 0.541 | | 3.0 | 0.136 |
| | | 0.80 | 7.1 | | 0.92 | 14.4 | |
| Maximum | Treatment** | | | 0.037 | | | 0.009 |
| | Site** | | 13.1 | 0.011 | | 23.0 | 0.003 |
| | T_{max} | | 0.1 | 0.762 | | 0.4 | 0.538 |
| | T_{max}*Treatment** | | 5.7 | 0.054 | | 8.4 | 0.028 |

If temperature-mediated competition caused zonation in our study system, we would expect brown trout to impart a negative impact (on cutthroat trout) at warm temperatures and cutthroat trout to do the same (to brown trout) at cool temperatures. Counter to this prediction, however, brown trout negatively impacted cutthroat trout under all but the warmest conditions in our experiment. Further, brown trout were unaffected by cutthroat trout at all temperatures. Thus, while we present evidence of a negative effect of exotic brown trout on native cutthroat trout, temperature-mediated competition does not satisfactorily explain zonation in our system. The observed segregation may instead be due to an abiotic determination of brown trout's upstream limit, coupled with their demonstrated ability to negatively impact cutthroat trout when they co-occur. Thus, we believe that brown trout have invaded as far upstream as is physiologically possible and during this process have displaced cutthroat trout from downstream reaches.

Table 3.5. Table summarizing experimental studies of temperature-mediated competition among salmonid species. 'species 1 > species 2' denotes that species 1 was a more successful competitor than species 2.

| Upstream species | Downstream species | Arena (density) | Temperature range | Performance measure(s) | Main result(s) | Reference |
|--|---|--|--|---|---|------------------------------|
| Cutthroat trout (<i>Oncorhynchus clarki pleuriticus</i>) | Brook trout (<i>Salvelinus fontinalis</i>) | 1.8 x 0.6 m lab stream (5.5 fish·m ⁻²) | Constant 10 and 20 °C | Aggressive acts; microhabitat use; frequency of dominance | Brook > cutthroat (all responses) at 20°C; At 10 °C, brook trout = cutthroat trout in microhabitat use and dominance frequency; There was temperature-mediation of aggression (i.e., brook trout were more aggressive at high and cutthroat trout at low temperatures). | Destaso and Rahel 1994 |
| Brook trout (<i>Salvelinus fontinalis</i>) | Rainbow trout (<i>O. mykiss</i>) | 1-m ² pools and riffles in a lab stream (2 fish·m ⁻²) | Constant 13 and 18 °C | Aggressive acts; food acquisition; growth | Brook trout > rainbow trout for all response measures at both 13 and 18 °C. | Magoulick and Wilzbach 1998b |
| Cutthroat trout (<i>O. c. pleuriticus</i>) | Brook trout (<i>Salvelinus fontinalis</i>) | 190-L lab aquaria (12.7 fish·m ⁻²) | Diel cycles of 1-8 and 9-17 °C | Food acquisition; aggressive acts; microhabitat use | Larger brook trout dominated overall, with greater aggression at 9-17 °C; Cutthroat trout never attained an advantage. | Novinger 2000 |
| White-spotted char (<i>Salvelinus leucomaenis</i>) | Dolly varden char (<i>Salvelinus malma</i>) | 2.8 x 0.35 m lab stream (51 fish·m ⁻²) | Constant 6 and 12 °C | Aggressive acts; foraging frequency; microhabitat use; growth; survival | White-spotted char generally dominated over dolly varden char across temperatures and responses; Their effect was diminished at 6 °C, suggesting a mediating role of temperature. | Taniguchi and Nakano 2000 |
| Brook trout (<i>Salvelinus fontinalis</i>) | Brown trout (<i>Salmo trutta</i>) | 2 x 0.6 m lab stream (2.5 fish·m ⁻²) | Constant 3, 6, 10, 20, 22, 24, and 26 °C | Food acquisition; aggressive acts | Brook = brown at all temperatures; Brook trout had greater mortality than brown trout due to high temperatures. | Taniguchi et al. 1998 |
| Cutthroat trout (<i>O. c. utah</i>) | Brown trout (<i>Salmo trutta</i>) | 20-m ² <i>in situ</i> enclosures (0.40 fish·m ²) | Ambient cycle range: mean: 8-13 °C; min-max: 6.1-17.5 °C; See Table 2. | Condition (validated as surrogate for growth) | Brown trout were unaffected by cutthroat trout; Cutthroat trout condition was reduced by brown trout at all temperatures, excluding 17.5 °C. | This study |

The role of temperature in zonation

Despite the absence of strong temperature effects, existing information suggests that temperatures measured in our experiment are limiting for brown trout at the cold extreme. First, a comparison of growth optima with observed temperatures indicates that high-elevation sites are likely too cold. Our two uppermost sites averaged only 8.1 °C (range: 6.1 - 11.2 °C) and 9.9 °C (6.9 - 13.8 °C), while brown trout optimum growth occurs between 13 - 18 °C (Elliot and Hurley 2000; Ojanguren et al. 2001). Accordingly, brown trout are rarely collected at long-term sampling stations near these two sites (De la Hoz Franco and Budy 2004; Budy et al. 2004; Figure 3.2). Analyses of broad-scale fish distributional patterns in the western U.S. further demonstrate a strong correlation between brown trout occurrence and a minimum temperature threshold (Vincent and Miller 1969; Rahel and Nibbelink 1999; but see Fausch 1989).

While data on the thermal physiology of Bonneville cutthroat trout are limited, our derived growth optimum (13 - 19 °C; See Materials and Methods) suggests that temperatures measured at the warmest of sites are optimal, rather than too warm, for this species. In fact, our estimated growth optimum includes the warmest maximum temperature measured in our trial. Recent studies also show that Bonneville cutthroat trout are well adapted to survive and grow at temperatures well in excess of those in our study (Wagner et al. 1998; Johnstone and Rahel 2003; Shrank et al. 2003). Thus, while we did not document a direct thermal control on either brown or cutthroat trout in our experiment, there is ample published information suggesting that the upper brown trout limit is defined by temperature while the lower limit of cutthroat trout clearly is not.

The role of biotic interactions in zonation

We provide evidence for an asymmetric, negative effect of brown trout presence on cutthroat trout. Allopatric cutthroat trout attained higher condition than did their sympatric counterparts at nearly all sites. Sympatric brown trout, in contrast, performed better than allopatric brown trout everywhere. Our use of a substitutive approach for assessing competition (Fausch 1998) indicates that interspecific competition (with brown trout) is more intense than intraspecific competition for cutthroat trout, while for brown trout the reverse is true. Further, the fact that the condition differential (between treatment groups) for brown trout was consistent (i.e., there was no reversal in competitive ability) at all temperatures suggests a lack of temperature-mediated competitive resistance to brown trout invasions by cutthroat trout.

While the potential for cutthroat trout displacement from downstream habitats due to brook trout invasions is widely acknowledged (Dunham et al. 2002; Novinger and Rahel 2003; Quist and Hubert 2004), the potential for a similar effect of brown trout is rarely considered. Distributional patterns in the Bonneville Basin (De la Hoz Franco and Budy 2004) indicate that displacement may have occurred, and we provide insight into a possible mechanism. While we did not document the behavioral origin of brown trout impacts in our study, dominance via aggression (i.e., interference competition) is a likely candidate. In a lab study of brown trout–greenback cutthroat trout (*O. c. pleuriticus*) interactions, brown trout were more aggressive, attained the best foraging positions, and thereby suppressed cutthroat trout feeding (Wang and White 1994). In other studies, brown trout dominated over masu salmon (*O. masou*), white-spotted char (*Salvelinus leucomaenis*), and were unaffected by steelhead trout (*O. mykiss*; Kocik and Taylor 1994; Hasegawa et al. 2004). Brown trout are thus well established as a dominant competitor among salmonids.

In sum, we believe the downstream limit of cutthroat trout is determined by the presence of and their interactions with brown trout. Further, the observation that brown trout performed consistently better with cutthroat trout in our experiment indicates that temperature rather than competitive resistance likely explains the absence of brown trout from high elevations.

Salmonid temperature-mediated competition experiments

Temperature-mediated competition has been proposed as the primary cause of salmonid zonation in rivers and streams throughout the world (Fausch 1989; Fausch et al. 1994; De la Hoz Franco and Budy 2004). In addition to our field experiment, this proposition has been evaluated for several salmonids using a variety of performance responses (Table 3.5). Encompassing a wide range of temperatures and experimental densities, a simultaneous consideration of these studies illustrates two patterns. First, downstream species are superior competitors in two-species systems (but see Magoulick and Wilzbach 1998b); and second, reversals in dominance due to cold temperatures – whereby the upstream species attains superiority – rarely occur (but see DeStaso and Rahel 1994).

The lack of a competitive reversal has been attributed to at least one of three causes. First, while competitive effects of downstream species may be dampened under cold conditions, temperatures may not have been sufficiently extreme to induce dominance reversals (Taniguchi et al. 1998; Taniguchi and Nakano 2000). The fact that reversals have not been observed at temperatures as low as 1-3 °C (see Table 3.5) indicates

that this explanation is unlikely. A common thermal physiology for both species might also prevent a competitive reversal (Novinger 2000). Given that thermal tolerance and temperature-related mortality differed among species in at least two studies (see Table 3.5) suggests that this, too, is an unlikely explanation.

Finally, the lack of a dominance reversal suggests that abiotic factors rather than temperature-mediated competition preclude downstream species from high-elevation reaches. Specifically, downstream species may be unable to avoid starvation (Taniguchi et al. 1998; Taniguchi and Nakano 2000) and/or complete their entire life cycle (e.g., embryonic phases; DeStaso and Rahel 1994; Novinger 2000) under cold conditions, even if juveniles or adults experience positive growth under short-term, experimental conditions. We believe that these are more plausible explanations for why reversals were rarely observed and are deserving of further scientific attention. In sum, our study adds to a growing body of evidence suggesting that salmonid zonation is not the result of condition-specific competition.

Implications for cutthroat trout conservation

The potential for negative effect of brown trout on cutthroat trout and the likely limitation of the present distribution of brown trout by abiotic conditions, have important implications for the conservation of cutthroat trout. First, management actions involving the direct removal of brown trout should be considered if increasing the abundance and spatial extent of cutthroat trout is desirable (e.g., Lentsch et al. 1997). Such actions have been aggressively pursued for the conservation of cutthroat trout in the presence of invasive brook trout (Thompson and Rahel 1996; Novinger and Rahel 2003; Peterson et al. 2004) and the demographic benefits (e.g., increased age-0 cutthroat trout survival) are promising (Peterson et al. 2004). Thus, the eradication of exotic brown trout may benefit cutthroat trout where these species co-occur.

While brown trout invasions may have slowed in streams like the Logan River (i.e., they have had ~100 years to invade suitable habitats), this may change under future climatic and land-management scenarios. If temperatures increase, brown trout distributions may shift upstream (Keleher and Rahel 1996) and thus reduce the extent of remaining cutthroat trout populations. Indeed, brown trout distributions have been observed to change rapidly in invaded systems during periods of climate change (e.g., drought; Closs and Lake 1996). While there is little managers can do to affect climate, they can take measures to reduce land-management related water temperature changes (e.g., changes in vegetation; Theurer et al. 1984).

In conclusion, brown trout effects are currently recognized as only a minor threat to cutthroat trout persistence (Quist and Hubert 2004) – secondarily to the respective hybridization and displacement impacts of rainbow and brook trout (Dunham et al. 2002; Weigel et al. 2003). However, we suggest that exotic brown trout invasions could have serious consequences for cutthroat trout. Thus, brown trout should be considered more explicitly in cutthroat trout conservation efforts.

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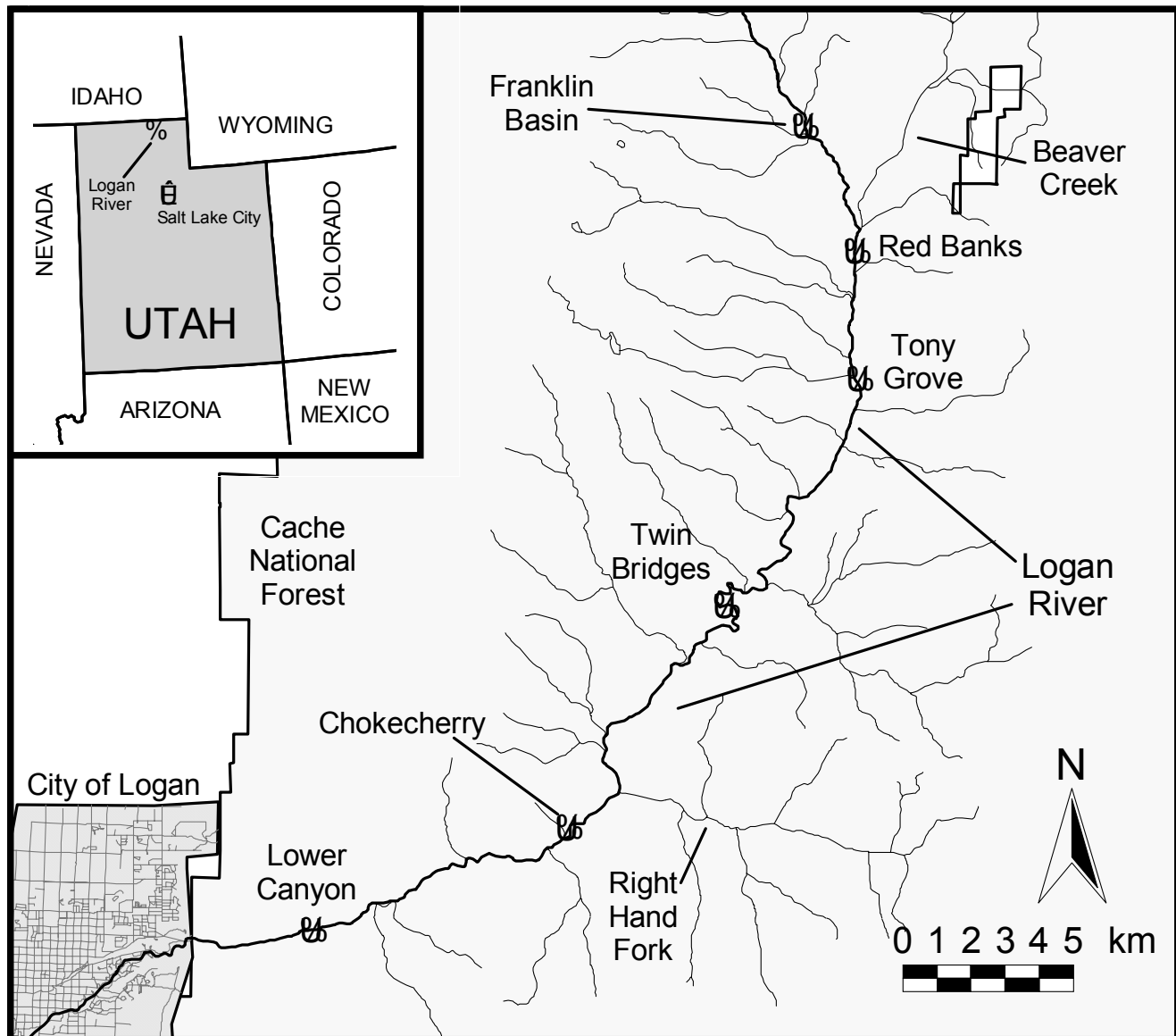


Figure 3.1. Map of the Logan River Drainage in northern Utah (41°44'N, 111°46'W). The experimental reach extends from the Idaho border (northern edge of detailed figure) to the lower end of U.S. Forest Service ownership (at the city boundary). Enclosure sites are labeled with site name. Experimental fish were collected from Right Hand Fork, Beaver Creek, and the mainstem Logan River upstream of the Franklin Basin site.

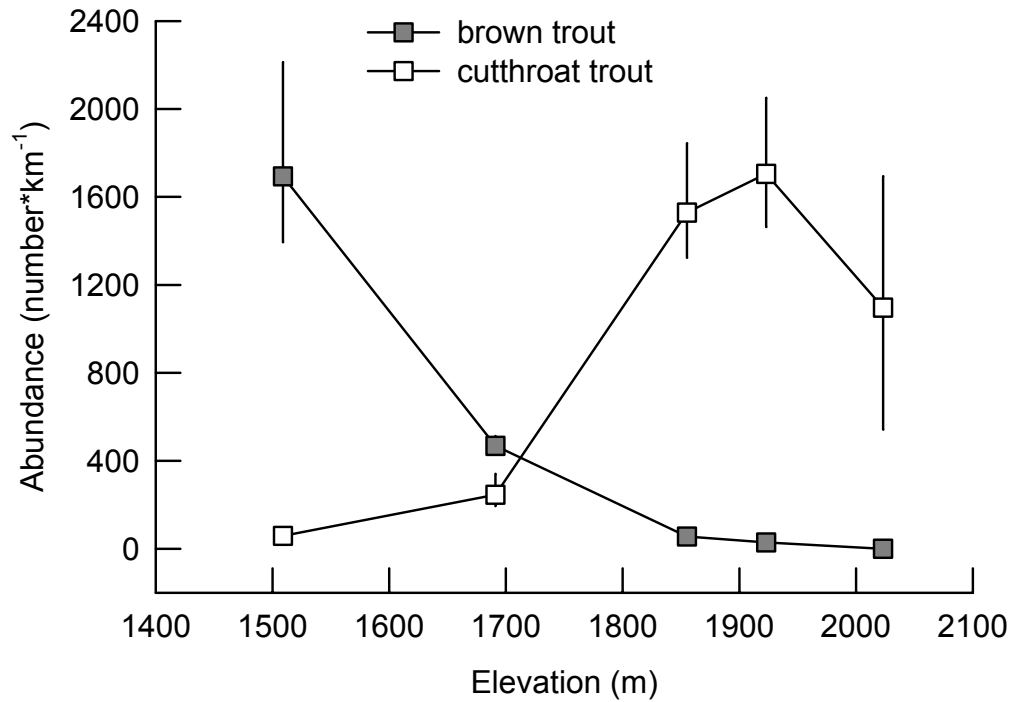


Figure 3.2. The brown trout-cutthroat trout altitudinal species-zonation pattern of the Logan River, Utah. Estimates of trout abundance are from Budy et al. (2004) and represent the mean (\pm range) based on three-pass electrofishing surveys made at five long-term monitoring sites in the summers of 2001-2003.

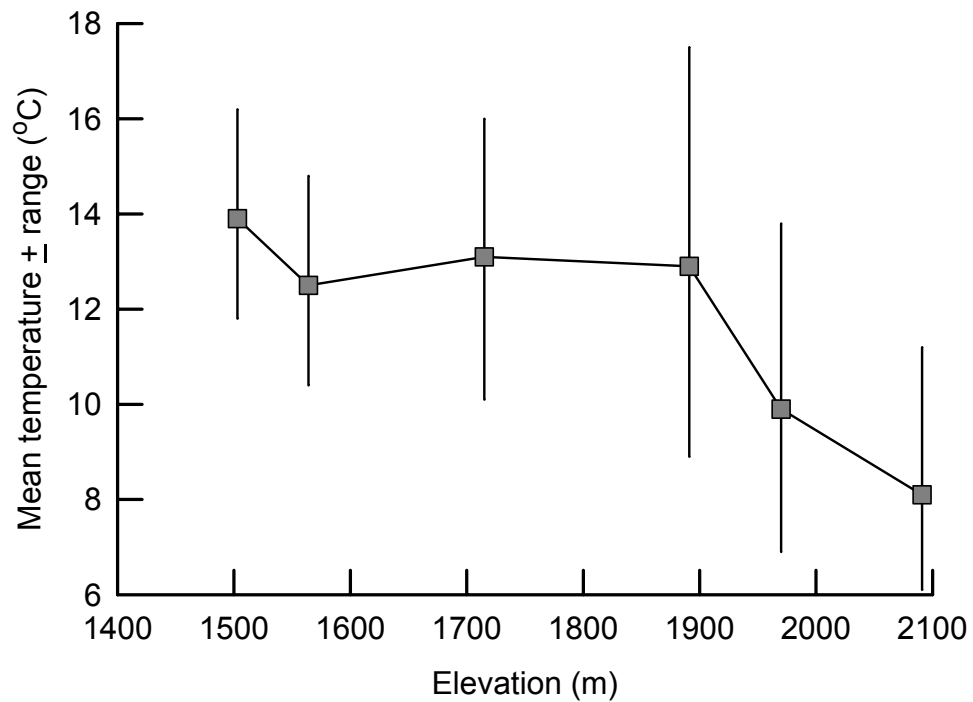


Figure 3.3. Mean temperature \pm range ($^{\circ}\text{C}$) during the trial period (14 July – 25 August 2003) plotted as a function of elevation. For reference, the temperature range of brown trout optimum growth is 13 - 18 $^{\circ}\text{C}$ while that of Bonneville cutthroat trout is 13 - 19 $^{\circ}\text{C}$ (see Methods for details on these ranges).

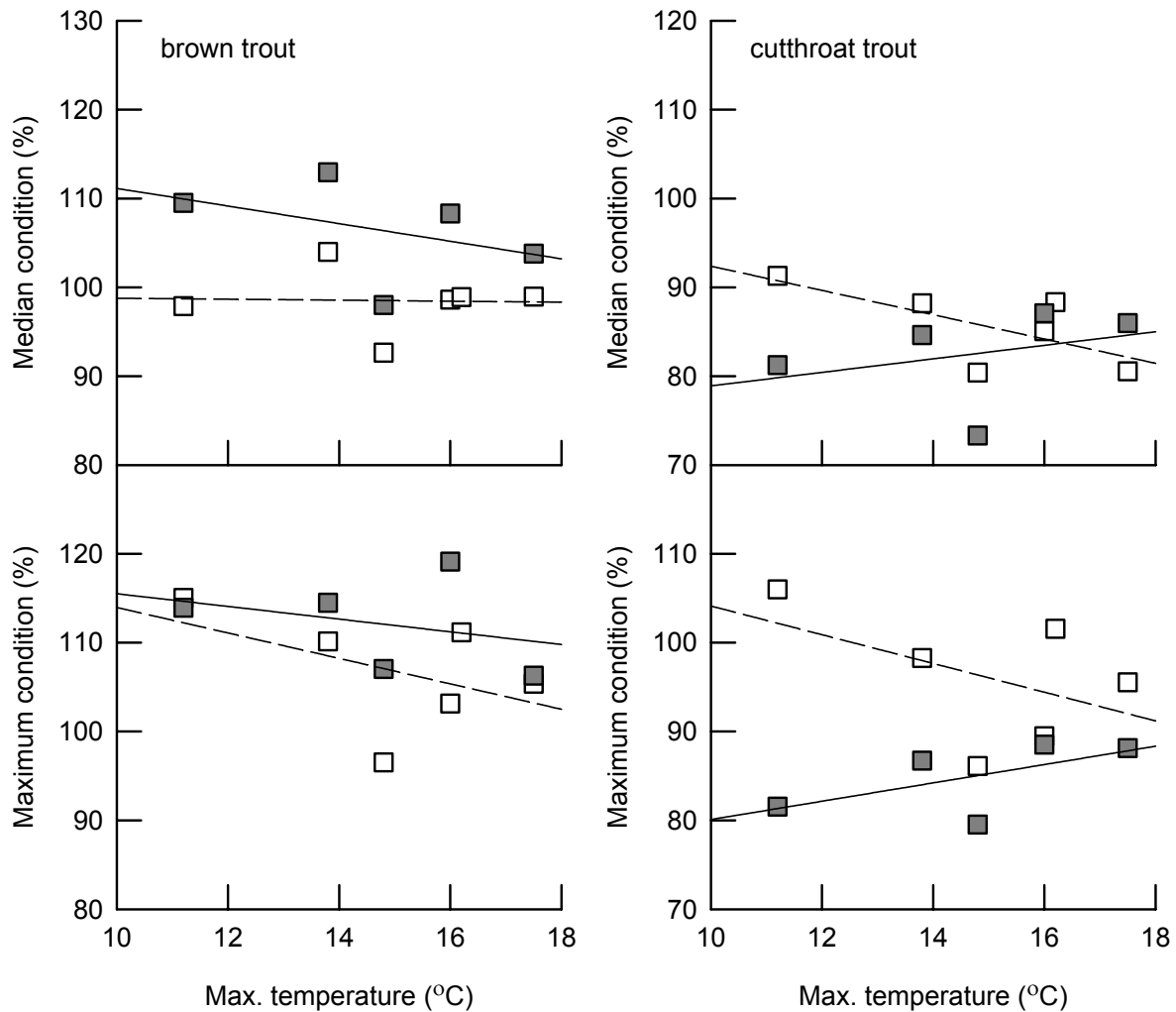


Figure 3.4. Median and maximum condition for brown trout (left panel) and cutthroat trout (right panel) plotted as a function of maximum water temperature during the trial period (°C). Symbols for sympatric and allopatric enclosures are black and white, respectively; the ANCOVA regression model for allopatric fish is the dashed line while that for sympatric fish is the solid line. Note: for clarity purposes, brown trout and cutthroat trout are plotted on y-scales with different minima and maxima but a constant range (50%).

CHAPTER 4:
A field-experimental assessment of individual- and population-level effects of brown trout on Bonneville cutthroat trout in northern Utah streams

INTRODUCTION

Exotic invasions pose a formidable threat to the persistence of native cutthroat trout (*Oncorhynchus clarki* subspecies) populations throughout western North America (Dunham et al. 2002). The impacts of introduced rainbow trout (*O. mykiss*; via hybridization, Weigel et al. 2003) and brook trout (*Salvelinus fontinalis*; via interspecific competition, Dunham et al. 2002) have caused the local extinction of many cutthroat trout populations and are thus regarded as a major conservation concern (Quist and Hubert 2004). Introduced brown trout (*Salmo trutta*) effects, in contrast, are considered by many to be of only minor importance to cutthroat trout conservation; recent investigations, however, suggest otherwise.

Observational and experimental studies on species distributions, abundance patterns, and interactions in northern Utah streams suggest that brown trout effects are considerable. First, brown and cutthroat trout segregate longitudinally in rivers where they co-occur (De la Hoz Franco and Budy 2005), a pattern suggestive of historical displacement (i.e., ‘the ghost of competition past’ Connell 1980). Further, in their analysis of factors explaining trout abundance in the Logan River, De la Hoz Franco and Budy (2005) demonstrated that cutthroat trout and brown trout abundance are strongly and negatively correlated. In addition to suggestive distributional patterns, we recently demonstrated the potential for negative effects of brown trout on cutthroat trout in a controlled, field-experimental setting (McHugh and Budy, *in revision*; see Chapter 3). By rearing both species in experimental sympatry and allopatry in stream enclosures, we demonstrated that the presence of brown trout can substantially reduce cutthroat trout growth and condition.

Despite compelling evidence indicating that brown trout should be regarded as a threat to native fish populations in Utah, there remain several questions that should be considered before a comprehensive brown trout management plan is developed. First, by confining mobile vertebrates to small-scale enclosures in our 2003 experiment (McHugh and Budy, *in revision*), we may have artificially intensified interactions to a level unrepresentative of those that occur in nature. Second and perhaps more importantly, it is possible that the suppression of individual-level cutthroat trout performance (i.e., growth and condition) by brown trout does not cause a concomitant population-level response (e.g., a reduction in survival; Taniguchi and Nakano 2000; Peterson and Fausch 2003). Given the depressed status of many

Bonneville cutthroat trout populations in Utah, addressing these issues and fully integrating them into a comprehensive strategy for cutthroat trout conservation in the presence of exotic brown trout is of paramount importance.

To address these unresolved issues we conducted another field experiment during the period extending from July 2004 to March 2005. Our main goal was to assess the effects of interactions within a more natural, large-scale setting and simultaneously consider both individual- and population-level performance measures. Within this, our objectives were: 1) to quantify the effects of brown trout on the individual- (growth, condition) and population-level (movement, survival) performance of cutthroat trout; and 2) to measure the response of cutthroat trout dietary habits in response to brown trout removal.

STUDY SITE

We conducted our experiment at three sites occupying two northern Utah streams, Rock (Upper Rock Creek, ROCU; Lower Rock Creek, ROCL) and Curtis creeks (CURT; Figure 4.1). We selected experimental sites based on four criteria: 1) they needed to contain both brown and cutthroat trout locally; 2) they had to be sufficiently small (2-4 m wide) to facilitate effective backpack electrofishing (for experimental set up) and accommodate the installation and use of small weirs (to isolate experimental reaches and monitor fish movements; described below); 3) they had to represent the spectrum of habitat conditions within which cutthroat trout are currently found in northern Utah; and 4) they needed to be of limited value to anglers and other outdoor recreationists (to minimize disturbance and vandalism).

The headwaters of Rock and Curtis creeks originate on the west slope of the Monte Cristo Range of northern Utah; both streams flow westward through narrow canyons towards a wide valley where they join the Blacksmith Fork River. While Rock and Curtis creeks are separated by only a few kilometers, they differ considerably in habitat conditions (Table 4.1; see Methods – Environmental variables for details). Specifically, Curtis Creek is much colder, larger, and steeper than either of the Rock Creek sites. The climate of the area is characterized by cold, snowy winters (January air temperature: low, -9 °C; high, 0 °C; mean precipitation 4.0 cm) and hot, dry summers (July air temperature: low, 15 °C; high, 31 °C; mean precipitation 1.6 cm), yielding a hydrograph dominated by a spring-snowmelt flood followed by base-flow conditions. Cutthroat trout, brown trout, and sculpin [*Cottus* spp.] comprise the fish fauna of both sites. Rock Creek additionally contains mountain suckers (*Catostomus platyrhynchus*) whereas Curtis Creek has a limited number of hybrid rainbow trout X

cutthroat trout (which were excluded from the experiment based on phenotypic characteristics).

METHODS

Experiment overview

Experimental design

We evaluated the effects of brown trout on both individual- and population-level performance of cutthroat trout following a strategy similar to that used in our 2003 study (McHugh and Budy, *in revision*; see Chapter 3). That is, we raised cutthroat trout in the presence and absence of brown trout according to a substitutive design (i.e., one based on equal total density but substitution of an individual fish's species identity; *sensu* Fausch 1998) and subsequently compared performance (growth, condition, movement, and survival) and dietary habits between treatment groups. In contrast to our 2003 study, however, we scaled our experimental unit upwards, using local 'populations' of trout occupying ~300-m stream reaches rather than small groups of fish in 20-m² enclosures. We replicated each treatment once at each of three sites following a randomized complete block design (site as the blocking factor). Thus, each treatment was replicated a total of three times.

Set-up procedures

Prior to setting up treatments within a site, we isolated two ~300-m reaches using two-way fish weirs equipped with bi-directional trap boxes (see Peterson et al. 2004 for details). Weirs were constructed out of 6.4-mm black plastic mesh and PVC and were secured to the streambed using rebar and plastic cable ties. To ensure that weirs were complete barriers to fish movement and thus effective at isolating reaches, we buried a 30-cm skirt around the base of each and inspected it underwater with a mask and snorkel. Following installation, we established treatments using two-pass backpack electrofishing methods (250-300 V, 30 Hz, 4 mS) in early July 2004. Thus, we netted and retained (in live wells) all trout encountered during two electrofishing passes of a given reach. Following anesthetization, we weighed, measured, tagged (cutthroat trout: PIT-tag and T-bar anchor tag; brown trout: T-bar anchor tag only), and marked (randomly assigned by treatment, anal or adipose fin clip) all cutthroat and brown trout that were captured and destined for inclusion in our experiment. Brown trout from cutthroat trout only reaches were weighed, measured, euthanized, and buried.

Following fish processing, we returned cutthroat trout only to the cutthroat alone reach; both species were returned to the cutthroat trout with brown trout reach. However, because we wanted to maintain a similar trout density between treatments (i.e., a substitutive design) and a roughly 50:50 brown-to-cutthroat-trout ratio – which none of the sites had initially (Table 4.2) – we had to augment releases of trout captured within experimental reaches with fish collected immediately up- and downstream of sites (i.e., non-experimental reaches within the same stream). By collecting supplementary fish nearby, we attempted to minimize the potential impacts this would have on results (e.g., movements). Finally, in order to maintain the natural size structure for both species in our study, we made no conscious manipulation of this aspect of experimental trout populations. Thus, with the exception of species composition, the fish population characteristics in our experimental reaches were reflective of those existing prior to experimental set up (Table 4.2).

Trial overview

Following the establishment of our last experimental population on 7 July 2004 (ROCL), the experimental trial period began. We cleaned and checked traps daily throughout a 72-day summer trial period. Otherwise, fish were allowed to interact with minimal disturbance during this time. We resampled all reaches (using two-pass electrofishing methods) during mid-September 2004 to gain information on summer growth and condition as well as dietary habits (isotopic measures). Following this sample event, trap operations were discontinued at Upper Rock and Curtis Creek sites and weirs were removed. In order to facilitate a thorough analysis of survival, however, we maintained Lower Rock Creek traps as barriers through March 2005. In addition to the post-summer ROCL sample occasion, we resampled (two-pass methods) this site on two other occasions (16 November 2004 and 15 March 2005). Thus, our experiment is characterized by two general periods, each with a different focus: 1) a 2.5-month summer period where growth, condition, movement, and dietary habits were assessed across three sites based on a single release and recapture occasion; 2) a 9-month summer-to-spring period where an intensive assessment of cutthroat trout survival at a single site was the main focus.

Cutthroat trout response variables

Individual-level performance measures

We evaluated the performance of individual cutthroat trout based on instantaneous growth (G) and condition (W_r , % relative weight). Instantaneous growth, G , was computed as

$$G = [(\ln W_{\text{final}} - \ln W_{\text{initial}}) \cdot t^{-1}] \cdot 100 \quad (1)$$

where W is the weight (mass) in grams and t is trial length in days. Additionally and using the same approach as in our 2003 experiment, we evaluated cutthroat trout condition using the relative weight index, W_r , where

$$W_r = W / W_s \cdot 100 \quad (2)$$

W is the observed weight of a given fish at the end of the trial, and W_s is its predicted weight (g) based on its measured total length (mm) and a 'standard' length-weight relationship for the species (McHugh and Budy, *in revision*; see Chapter 3). Because the W_r and G distributions were skewed, we summarized individual-level performance for each local population (i.e., by site and treatment) using the median value. We evaluated W_r and G for each treatment population at all three sites for the summer period.

Dietary habits

In addition to assessing the impact of brown trout on cutthroat trout performance, we were also interested in identifying possible mechanisms for any effects observed. For this reason, we evaluated dietary patterns of cutthroat trout raised alone, cutthroat trout raised with brown trout, and brown trout raised alone. We did this using a stable isotope-based approach, a well-established method for assessing feeding habits and relations among aquatic organisms. Thus, we collected dorsal muscle tissue from cutthroat ($n = 5$ cutthroat from both treatments at each site) and brown trout ($n = 5$ from cutthroat with brown trout reach) that were captured during our mid-September sample event for isotopic analysis. We dried tissue samples for 24-48 h at 60°C and encapsulated them in tin capsules prior to shipping them to the UC-Davis Stable Isotope Facility (UCD-SIF) for analysis. The UCD-SIF quantifies the per mil concentration (relative to a standard) of ^{15}N and ^{13}C using mass spectrometry methods. Using isotope data, one can infer the trophic position (^{15}N) of different organisms as well as assess the extent of dietary overlap among organisms within trophic levels (^{13}C). In order to compare patterns, we summarized dietary patterns using mean ^{15}N and ^{13}C values ($\pm 2\text{SE}$) for each species, by site and treatment.

Population-level performance measures

The population-level response of cutthroat trout to brown trout presence was assessed using two demographic parameters: movement and survival. We computed

movement based on the proportion of unique recaptures (i.e., N marked fish recaptured in traps / N marked fish released) made at weirs (at upstream and downstream ends of reaches) during the 74-day summer trial period. Due to the possible influence of electrofishing and fish transfer on movement patterns, however, we only included recaptures observed ≥ 1 week after reach set up. Further, in order to maintain species composition constant throughout our experiment, we did not allow 'emigrants' to actually leave upon recapture, nor did we allow 'immigrants' to enter reaches (non-experimental fish were shuttled around experimental reaches in buckets); all experimental fish recaptured in traps were released at the midpoint of their reach of origin. Thus, ours is a measure of a population's propensity for movement rather than an actual immigration or emigration rate. We assessed this parameter for both treatments at all sites.

We assessed the impact of brown trout on cutthroat trout survival using a Cormack-Jolly-Seber survival modeling approach in Program MARK (White and Burnham 1999). Under this strategy, one can assess the influence of treatment effects and/or individual covariates (e.g., total length) on survival and simultaneously estimate relevant parameters (i.e., survival and recapture probability). However, a binary encounter history ('0' = not encountered, '1' = encountered) for a minimum of three encounter occasions (i.e., one release and two recapture events) is required for each fish in order to use this approach. Because we removed weirs on 15 September 2004 at Upper Rock and Curtis Creek sites following only a single post-summer recapture event, we could not perform a formal survival analysis for these sites; thus, our survival assessment is for Lower Rock Creek only. In Lower Rock Creek, we assembled encounter history files for each marked cutthroat trout based on one release (7 July 2004) and three recapture occasions (15 September and 15 November 2004, and 15 March 2005). While our survival analysis is still in progress, we provide preliminary estimates of survival and capture probability for each treatment group that were estimated using maximum-likelihood methods in Program MARK.

Environmental variable measurement

In order to evaluate the effects of environmental factors on cutthroat trout performance and to characterize differences in habitat conditions across sample sites, we measured several habitat characteristics at both the site and reach levels.

Site-level variables

Elevation and reach slope—Elevation (m) and slope (m/m) were measured from 7.5-minute USGS topographical maps and are expressed as site averages.

Discharge—We quantified discharge at the site level using a single base-flow discharge measurement made with an electromagnetic flow meter following standard USGS procedures. Additionally, we evaluated the trend in flows across the trial period using real-time USGS flow data collected on the mainstem Blacksmith Fork River (downstream from the study area; station number 10113500) during the period extending from 30 March 2004 to 21 March 2005.

Temperature—Water temperature was measured hourly during the 74-day trial period using a single data logger deployed at the middle of each site. Data were summarized using 74-day mean, minimum, and maximum temperature values.

Reach-level variables

All reach-level variables were measured during a habitat survey conducted within each reach immediately after weir installation and just before treatment establishment (late June 2004).

Reach length and width—The thalweg length (m) of each reach (downstream weir to upstream weir) was measured using a tape measure. Wetted width was measured at 20-30 systematically spaced (10-m intervals) locations along the length of each reach.

Large woody debris (LWD) abundance—We counted all large woody debris pieces (\geq 1-m length, \geq 10-cm diameter) located within the bankfull channel encountered during our survey. LWD data were standardized to a per-kilometer value.

Percent overhanging vegetation and undercut banks—We noted the presence or absence of overhanging vegetation (with \geq 0.5 m overhang, within \leq 1 m of the water's surface) and/or undercut banks (with \geq 5 cm lateral depth) at each width cross section (i.e., at 10-m intervals). From these data, we computed the percent of cross sections with overhanging vegetation and undercut banks present for each the left and right bank; the value given in Table 4.1 is the average of both banks.

Substrate variables—We quantified the median particle size (D50, mm) and percentage of fine sediments ($<$ 4 mm, the smallest particle effectively handled and measured) using the Wolman pebble count technique. We conducted a separate

pebble count on each of two riffles (one ~100 and the other ~200 m upstream from the downstream end of a reach) within each reach. Under this approach, we measured the intermediate axis of at least 100 blindly selected particles using a hand ruler.

Pool variables—We considered pools those habitat units characterized by slow water velocities with an upstream break in slope, a downstream hydraulic control (i.e., bathtub shaped), a length at least as long as the channel width, and a maximum depth at least 1.5 times the pool-tail crest depth. We assessed residual pool depth (cm) as the difference between maximum depth and pool-tail crest depth. Pool size (m²) was estimated based on the unit length and average width measurements (minimum of two). Percent pools was computed as the length of the entire reach that was occupied by pool habitats. Finally, the per-km frequency of pools was estimated based on the pool count per reach.

Table 4.1. Physical habitat conditions by treatment (cutthroat alone = ‘CUT alone’; cutthroat with brown trout = ‘CUT w/ browns’) and site. The upper and lower fields are site- and reach-level characteristics, respectively. NA = not applicable.

| Habitat variable | Curtis Cr. | | Upper Rock Cr. | | Lower Rock Cr. | |
|-----------------------------|------------|---------------|----------------|---------------|----------------|---------------|
| | CUT alone | CUT w/ browns | CUT alone | CUT w/ browns | CUT alone | CUT w/ browns |
| Elevation (m) | 1,758 | 1,758 | 1,818 | 1,818 | 1,697 | 1,697 |
| Slope (m/m) | 0.037 | 0.037 | 0.014 | 0.014 | 0.023 | 0.023 |
| Discharge (cfs) | 6.8 | 6.8 | 2.4 | 2.4 | 2.4 | 2.4 |
| Mean T (°C) | 11.1 | 11.1 | 15.9 | 15.9 | 16.7 | 16.7 |
| Min T (°C) | 6.6 | 6.6 | 8.0 | 8.0 | 8.9 | 8.9 |
| Max T (°C) | 17.3 | 17.3 | 23.5 | 23.5 | 24.5 | 24.5 |
| Reach Length (m) | 223 | 261 | 314 | 310 | 390 | 355 |
| Width (m) | 3.9 | 4.7 | 2.6 | 2.8 | 3.2 | 3.0 |
| LWD (pcs/km) | 313 | 287 | 70 | 39 | 131 | 245 |
| % Overhanging Veg. | 26 | 48 | 31 | 15 | 76 | 50 |
| % Undercut Banks | 26 | 33 | 19 | 24 | 29 | 20 |
| D50 (mm) | 64 | 45 | 5 | 34 | 18 | 28 |
| % Fines | 13 | 13 | 50 | 19 | 24 | 23 |
| Pool Depth (cm) | 23 | 26 | 33 | 35 | 23 | 24 |
| Pool size (m ²) | 19 | 22 | 28 | 27 | 22 | 15 |
| % Pools | 31 | 35 | 50 | 61 | 29 | 44 |
| Pools/km | 58 | 50 | 61 | 55 | 38 | 68 |

RESULTS and DISCUSSION

Trial overview

We successfully installed weirs, characterized physical habitat conditions, and established experimental populations in every reach by 7 July 2004. In total, we marked and released 207 cutthroat trout across the three sites. Our experimental manipulations clearly altered the species composition of each reach (Table 4.2); however, we were unable to remove every brown trout from the cutthroat trout only reach during the set-up phase; this was presumably due to brown trout's use of complex habitats as refugia from netting as well as the reduced efficiency of our electroshocker during the higher flow set-up period (Figure 4.2). While treatments were not perfectly substitutive in nature (see Experimental Design above) and brown trout were present in the cutthroat alone reach, the disparity of brown trout abundance between treatments was considerable. Thus, we will refer to treatment groups as cutthroat trout alone and cutthroat trout with brown trout throughout the remainder of this report.

Table 4.2. Fish population characteristics for replicate reaches, by site and treatment (cutthroat alone = 'CUT alone'; cutthroat with brown trout = 'CUT w/ browns'). 'BNT' = brown trout.

| Population characteristic | Curtis Cr. | | Upper Rock Cr. | | Lower Rock Cr. | |
|---|------------------|------------------|----------------|------------------|------------------|------------------|
| | CUT alone | CUT w/ browns | CUT alone | CUT w/ browns | CUT alone | CUT w/ browns |
| Pre-treat. BNT density (95% CI) ^a | 73 (49-166) | 50 (50-53) | 71 (70-74) | 76 (60-120) | 121 (113-137) | 157 (146-178) |
| Post-treat BNT density (95% CI) ^b | 45 (45-49) | 185 (169-215) | 42 (33-68) | 128 (118-147) | 29 (29-32) | 149 (126-192) |
| Pre-treat. CUT density (95% CI) ^a | 125 (112-155) | 138 (112-170) | 17 (16-23) | 31 (28-41) | 41 (41-43) | 30 (28-38) |
| Post-treat. CUT density (95% CI) ^b | 274 (260-286) | 300 (276-337) | 93 (92-96) | 82 (82-85) | 71 (67-83) | 54 (45-81) |
| CUT marked in July | 47 | 28 | 31 | 16 | 57 | 28 |
| CUT recaptured in September | 36 | 25 | 19 | 12 | 31 | 25 |
| Median CUT TL (mm) in July (2SE) | 250 (13) | 257 (19) | 220 (18) | 225 (28) | 223 (13) | 197 (17) |
| Median BNT TL (mm) in July (2SE) | NA | 263 (19) | NA | 166 (20) | NA | 197 (17) |

a. Based on 2-pass depletion estimate using data collected during the early July set-up phase.

b. Based on 2-pass depletion estimate using data collected during the mid-September recapture phase.

Environmental variables

Habitat conditions varied considerably across the six experimental reaches, but were consistent within sites (Table 4.1). Curtis Creek was larger (flow and width), colder (minimum, mean, and maximum temperature), steeper, and generally more complex (LWD abundance, undercut banks, D50) than either of the Rock Creek sites. Despite the fact that they were located within the same stream, Upper and Lower Rock Creek sites differed considerably. Specifically, ROCU was lower in slope and characterized by a classic pool-riffle channel, whereas ROCL was more step-pool like. Further, while ROCU had deeper pools on average, it was depauperate in LWD and overhanging vegetation relative to ROCL. For a more detailed account of habitat survey findings, see Table 4.1. See Figures 4.2 and 4.3 for the hydrograph and thermograph observed during the trial period.

Table 4.3. Individual- (growth, condition) and population-level measures (movement, survival; 2SE) of cutthroat trout growth by site and treatment (cutthroat alone = 'CUT alone'; cutthroat with brown trout = 'CUT w/ browns'). See field entitled 'CUT recaptured in September' in Table 4.2 for sample sizes used in calculations. NA = not applicable.

| Performance measure | Curtis Cr. | | Upper Rock Cr. | | Lower Rock Cr. | |
|--|------------------|------------------|------------------|------------------|------------------|-------------------|
| | CUT alone | CUT w/ browns | CUT alone | CUT w/ browns | CUT alone | CUT w/ browns |
| Median growth (g/g/day x 100) | 0.069 (0.056) | 0.002 (0.060) | 0.143 (0.102) | 0.100 (0.070) | 0.019 (0.042) | -0.014 (0.054) |
| Median condition (%) | 91.5 (2.4) | 91.2 (2.8) | 92.8 (5.0) | 82.4 (6.0) | 83.2 (2.0) | 82.8 (3.4) |
| Movement rate (July to September 2004) | 0.15 (0.10) | 0.11 (0.12) | 0.26 (0.16) | 0.19 (0.20) | 0.16 (0.10) | 0.03 (0.07) |
| Survival (July 2004 to March 2005) | NA | NA | NA | NA | 0.79 (0.07) | 0.77 (0.10) |

Cutthroat trout response variables

Individual-level performance measures

Across all three sites, individual cutthroat trout performed better alone than they did in the presence of brown trout (Table 4.3). Cutthroat trout instantaneous growth (Figure 4.4) averaged 0.077 and 0.029 % per day when alone and when in the presence of brown trout, respectively. Thus, brown trout reduced cutthroat trout growth to a level

half that observed in their absence. In contrast to growth effects, the response of cutthroat trout condition to brown trout presence was minor (Table 4.3, Figure 4.4). Though median condition averaged approximately 5% higher for cutthroat trout alone relative to cutthroat trout with brown trout (89 vs. 84%) across the three sites, this difference was driven almost solely by differences between treatments at ROCU. Within CURT and ROCL sites, the condition improvement due to the removal of brown trout was about 1%. Overall, however, there was a clear tendency for improved individual cutthroat trout performance in the absence of brown trout.

Though growth rates and condition values observed in the present study were considerably less than those observed in the Logan River during our 2003 enclosure experiment (McHugh and Budy, *in revision*; see Chapter 3), the tendency for suppression of individual cutthroat trout performance by brown trout was consistent between studies. Thus, brown trout effects scale upwards from small-enclosure to whole-reach experiments.

Dietary habits

Stable isotope-based analyses of dietary habits demonstrated two general patterns of significance to brown trout-cutthroat trout interactions (Figure 4.5). With respect to trends in ^{15}N first, it is clear that cutthroat trout alone, cutthroat trout with brown trout, and brown trout all feed at a similar trophic level in the ROCL, ROCU, and CURT food webs (i.e., they're all within $< 3\text{‰}$ ^{15}N of each other). Second and more importantly, we observed a clear tendency for a diet shift by cutthroat trout in the presence of brown trout. With respect to ^{13}C , we observed a clear shift in cutthroat trout diet in the presence of brown trout. This pattern was particularly striking for both ROCL and ROCU sites, and less so for CURT. When raised alone, cutthroat trout consumed a diet similar to that of brown trout. When raised with brown trout, however, cutthroat trout demonstrated a shift in diet (zero overlap in confidence intervals; Figure 4.5). Overall, these data suggest that interspecific interactions cause a shift in foraging and/or prey selection behavior of cutthroat trout. However, additional studies are needed to validate these dietary results (i.e., including direct observations of cutthroat trout feeding behavior alone and with brown trout and gut content analysis-based corroborations of isotopic results; see Chapter 2, *this report*).

Population-level performance measures

Brown trout impacted cutthroat trout movement rates considerably and survival rates marginally. First, brown trout clearly suppressed cutthroat trout movement rates (Table 4.3, Figure 4.6). When averaged across the three sites, cutthroat trout alone moved at a rate nearly double that of cutthroat trout with brown trout (0.19 vs. 0.11). The trend towards higher movement rates when alone was consistent across the three sites. However, movement rates tended to be low overall. On average, only 15% of marked cutthroat trout were recaptured at weir sites during the 74-day period.

We saw evidence of only a marginal effect of brown trout on cutthroat trout survival in our preliminary model-based analysis of Lower Rock Creek mark-recapture data (Table 4.3, Figure 4.7). Specifically, survival was only 2% higher for cutthroat trout in the absence of brown trout (0.79 vs. 0.77) and uncertainty around estimates was considerable for both treatment groups. In contrast, recapture probabilities differed considerably between groups (estimate [2SE]: 0.83 [0.09] vs. 0.97 [0.05]); the mechanism for this difference is unclear at this time but will be evaluated experimentally during the summer of 2005.

CONCLUSIONS

Our reach-scale experimental study on the effects of brown trout on cutthroat trout corroborates and extends the findings of our 2003 enclosure experiment. Specifically, we demonstrated that the growth and condition impacts of brown trout on cutthroat trout observed in small enclosures previously were analogous in an unconfined, natural river-reach setting. Additionally, we provide novel isotope-based evidence suggesting that changes in diet may be responsible for individual-level effects observed. Considering these results and those of our 2003 experiment, we conclude that brown trout's effect on individual-level cutthroat trout performance is well established and likely ubiquitous.

Based on the recommendations of Peterson and Fausch (2003), we also sought to evaluate impacts of brown trout on the population-level performance of cutthroat trout in the present study. With respect to movement patterns, we conclude that brown trout can significantly suppress the movement of cutthroat trout in natural habitats. Though we have not fully considered the demographic consequences or mechanistic causes of this result, we will explore the effects of interactions on movement in more detail during the summer of 2005 (see Future Work below). In contrast to the clear effects of brown trout on cutthroat trout movement, our preliminary survival analysis suggests that brown trout have only minor effects on cutthroat trout survival. We

caution, however, that this conclusion is tentative given that survival results were only available for one of our sites and for only one year. Further, the fact that the tendency was for improved survival by cutthroat trout alone relative to cutthroat trout with brown trout is consistent with the individual-level effects we observed. Additional sampling (see Future Work below) across all sites may allow us to estimate survival for all sites and thus formulate stronger conclusions regarding this parameter.

FUTURE WORK

Additional work is planned to help resolve uncertainties and more fully understand the experimental results described herein. First, we hope to sample all three sites in July 2005 in order to gain a full year's perspective on the survival and growth of marked fish. However, because fish have had the opportunity to leave experimental reaches since the time of weir removal, we caution that this sampling will be primarily exploratory in nature. Second, upon collection of these data we will perform a more formal analysis of survival models (for all sites) using a model-selection and multi-model inference approach. In addition to conducting additional work relating to our reach-scale experiment, we intend to extend our multi-scale assessment of brown trout-cutthroat trout interactions through a final, fine-scale lab experiment.

As the final experimental component of our multi-scale assessment of brown trout-cutthroat trout interactions, we will study the behavioral mechanisms responsible for the individual- and population-level effects documented in our enclosure and reach-scale studies to date. To do this, we will replicate the same basic experimental design (i.e., substitutive) in an artificial laboratory stream using wild brown and cutthroat trout. In contrast to our other experiments, we will focus on quantifying and comparing the behavioral interactions (e.g., aggressive encounters), dietary habits (i.e., floating vs. drifting prey), and habitat use patterns of cutthroat trout in the presence and absence of brown trout. This work will be scheduled for completion by August 2005.

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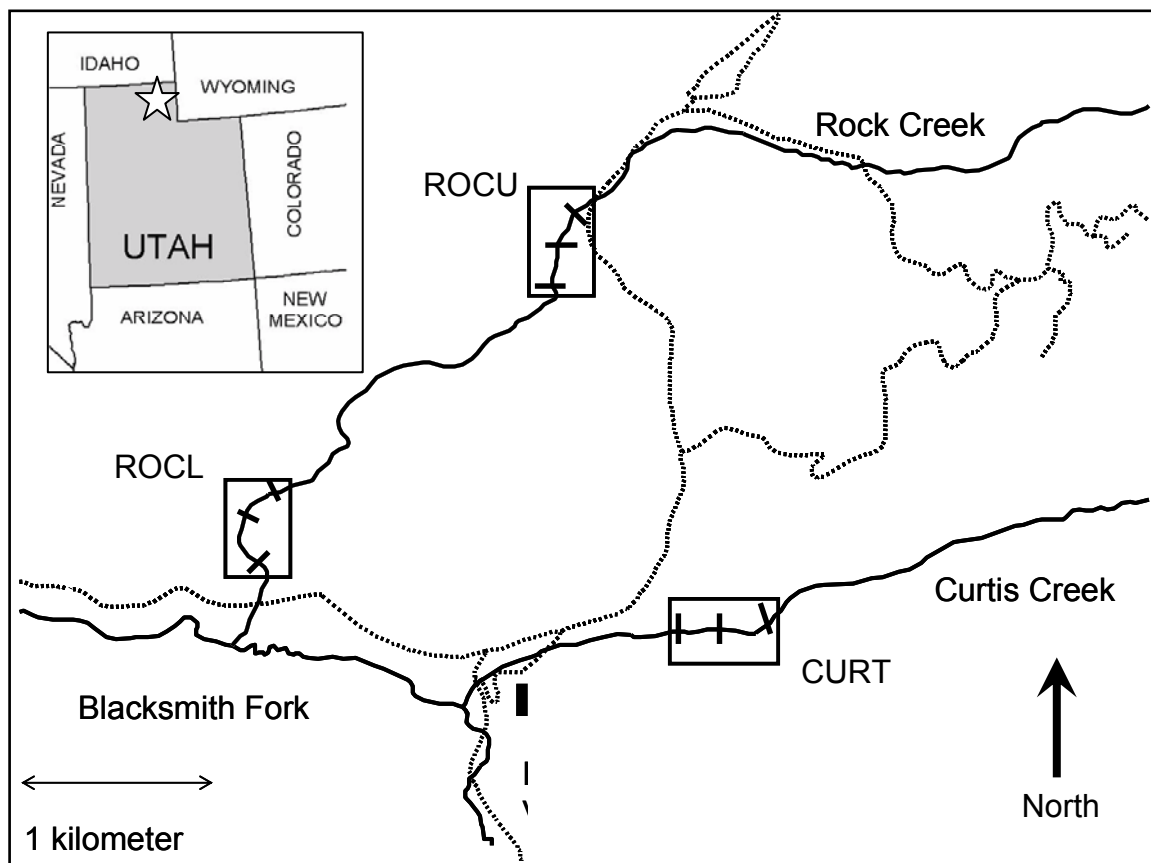


Figure 4.1. Map of the study area. The enclosed reaches with small hatches (= two-way traps) correspond to the locations of experimental sites in Upper Rock Creek ('ROCU'), Lower Rock Creek ('ROCL'), and Curtis Creek ('CURT'). The flow direction of all streams is westward.



Figure 4.2. The hydrograph for the main stem Blacksmith Fork River for the period extending from April 2004 - April 2005 (i.e., the period of preliminary surveys, experimental set-up, summer trials, and extended trap operations in ROCL).

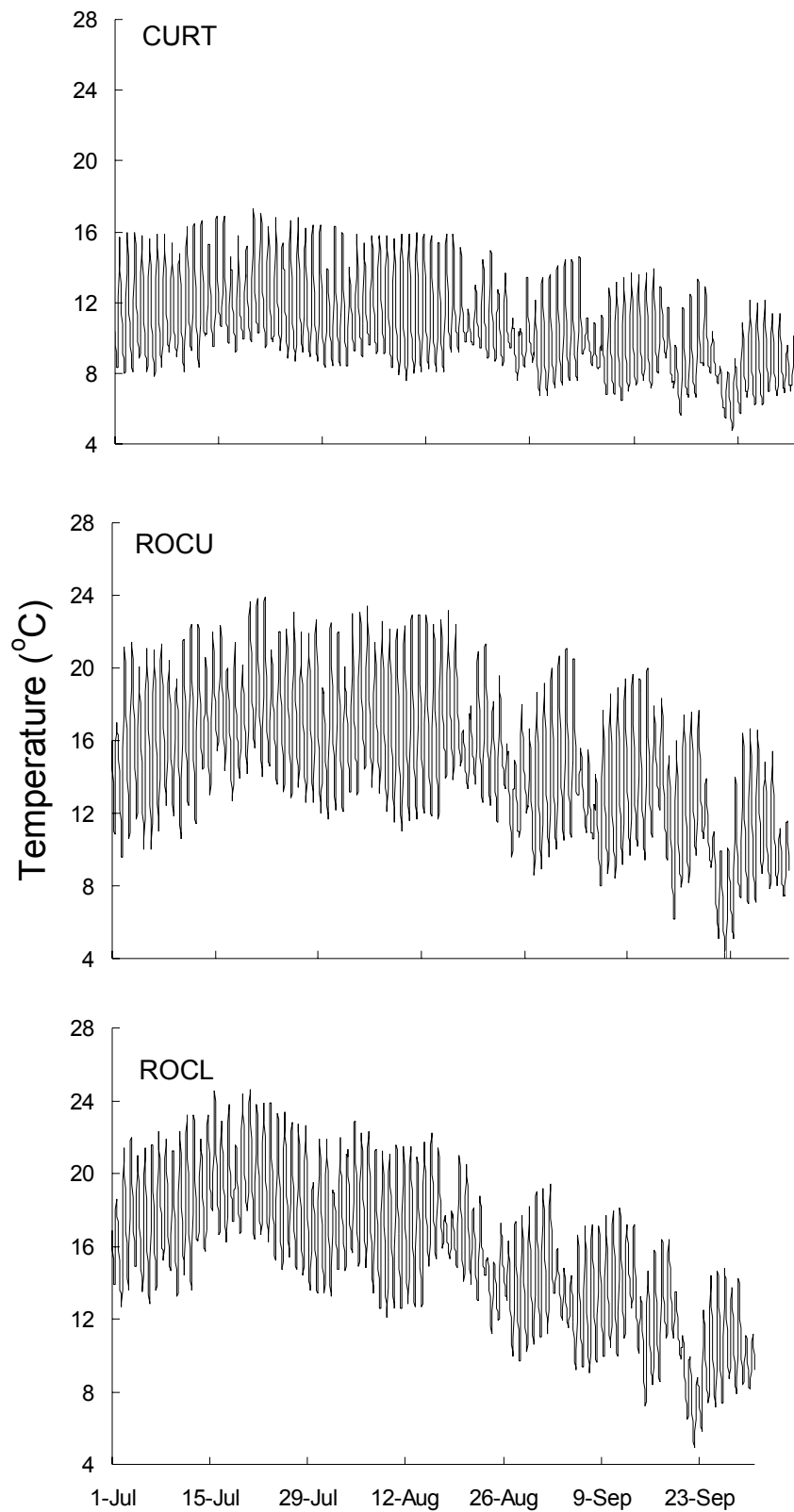


Figure 4.3. Thermograph for the three experimental sites during the 2004 summer experimental period.

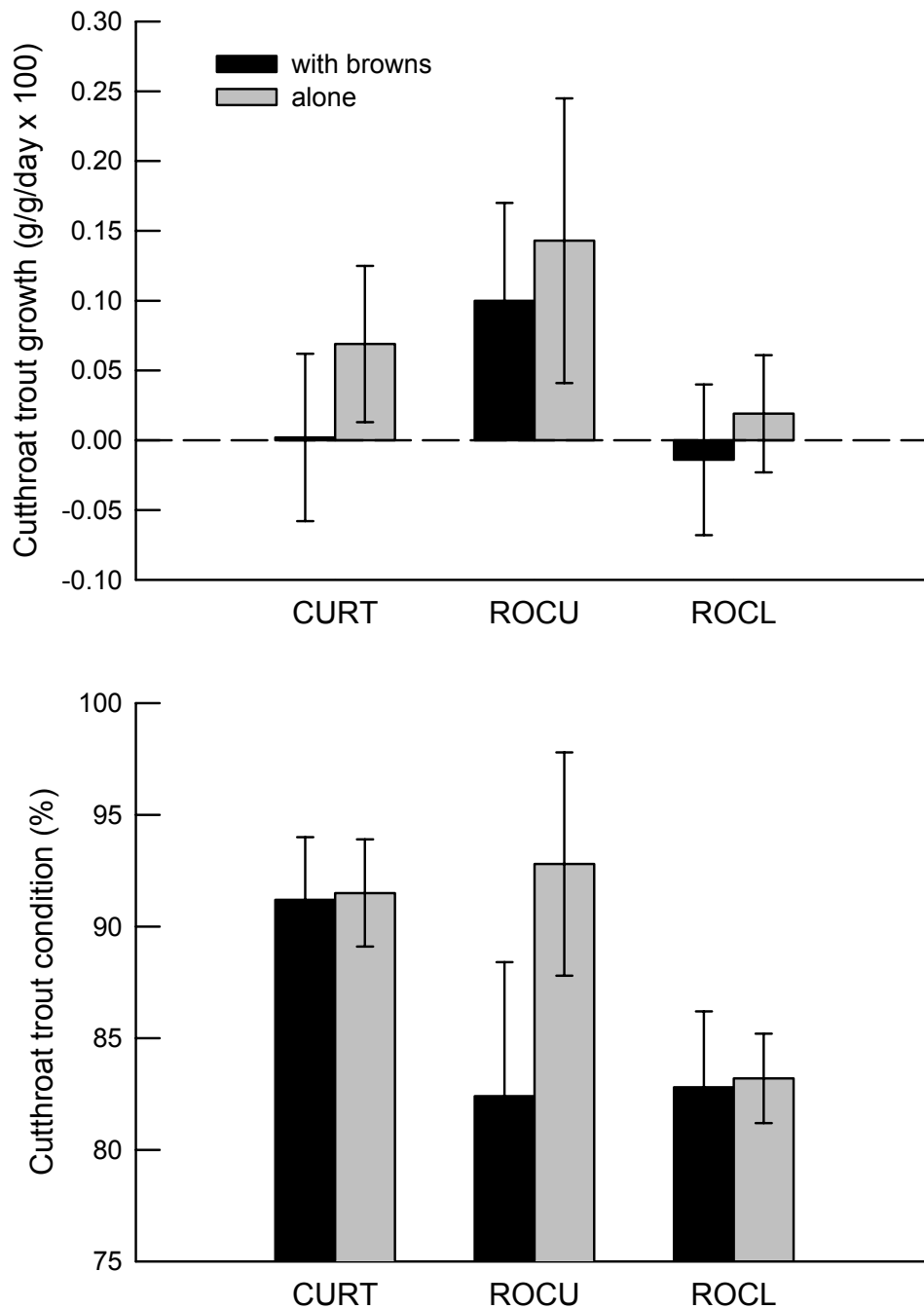


Figure 4.4. Individual-level measures (median growth ± 2 SE [g/g/day x 100], upper panel; median condition ± 2 SE [% relative weight], lower panel) of cutthroat trout performance in the presence (black bars) and absence (gray bars) across the three experimental sites ('CURT' = Curtis Creek; 'ROCU' = Upper Rock Creek; 'ROCL' = Lower Rock Creek).

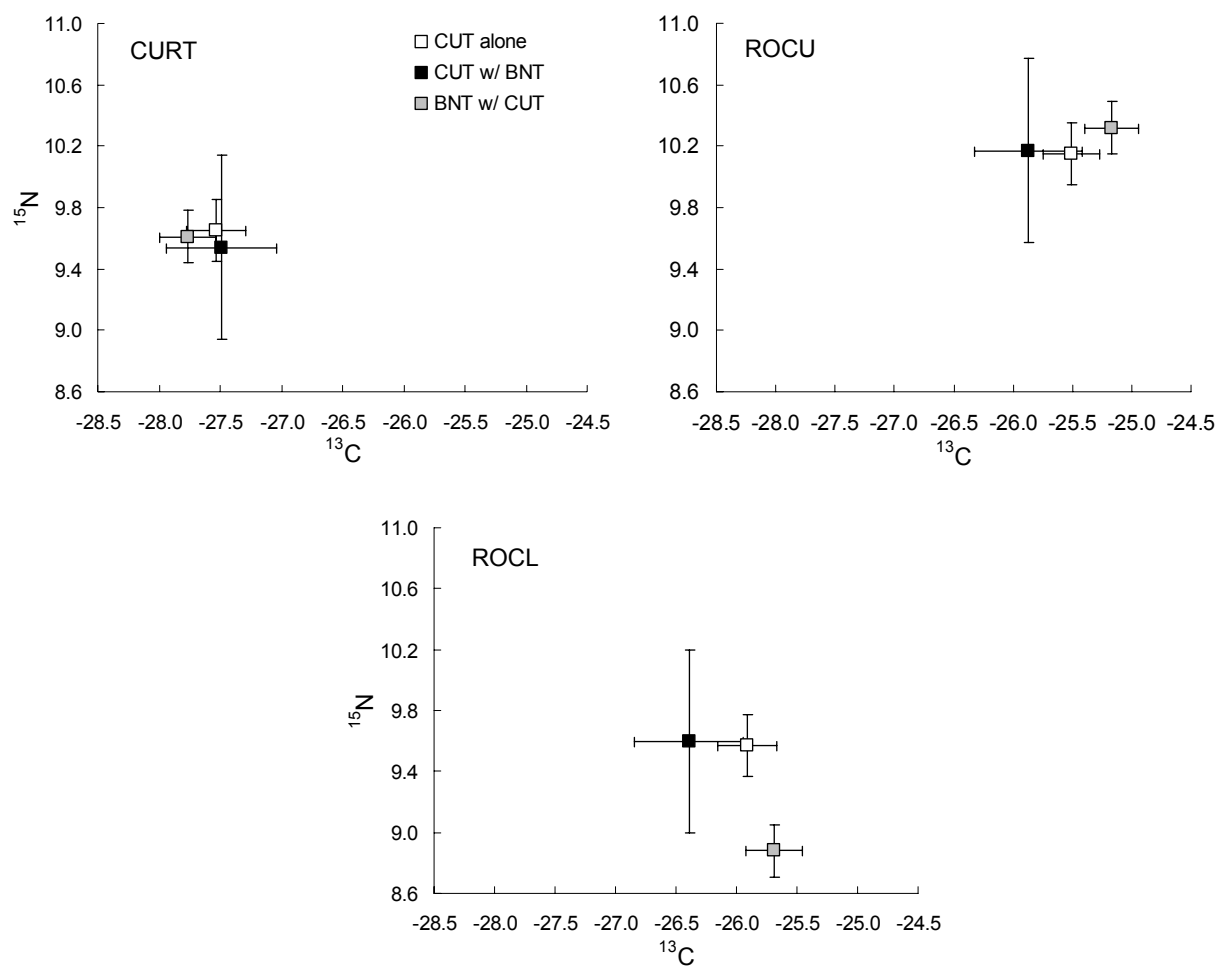


Figure 4.5. Stable isotope (^{15}N and ^{13}C , mean \pm 2SE) composition of experimental cutthroat trout (n = 5 alone ['CUT alone'], white squares; n = 5 with brown trout ['w/ BNT'], black squares) and brown trout (n = 5 with cutthroat trout ['w/ CUT'], gray squares).

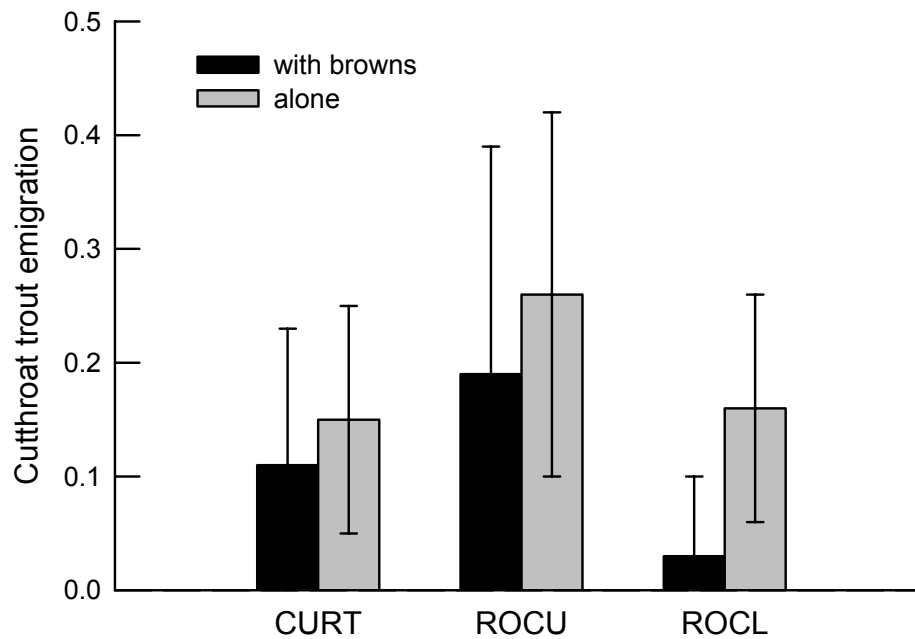


Figure 4.6. Cutthroat trout movement rates (± 2 SE [proportion of marked fish recaptured in traps during summer]) when in the presence (black bars) and absence (gray bars) of brown trout across the three experimental sites ('CURT' = Curtis Creek; 'ROCU' = Upper Rock Creek; 'ROCL' = Lower Rock Creek).

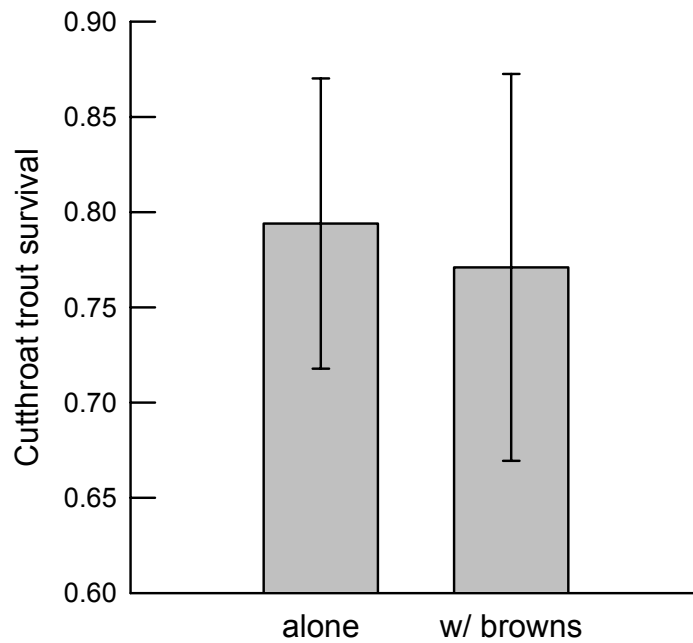


Figure 4.7. Cutthroat trout survival rates ($\pm 2 SE$) when in the presence ('w/ browns') and absence ('alone') of brown trout during the period 7 July 2004 – 15 March 2005. Values were estimated using a Cormack-Jolly-Seber model (Program MARK) with unique survival and recapture probabilities fit for each treatment group. Data are for ROCL only.

CHAPTER 5:

Modeling the synergistic effects of an emergent disease, physical factors, and species interactions on the survival and status of an endemic and imperiled fish

INTRODUCTION

The individual fate of an animal is often determined not by a single factor operating in isolation, but instead by the combined effects of many biotic and abiotic factors operating in combination (Figure 5.1). Synergistic effects of several factors operating together, such as disease and predation, for example, may result in mortality, and eventually population-level extinction, that may not have occurred in the presence of only one threat or factor alone (e.g., Lake Malawi, snail predators, *Schistosomiasis*, Wilson 2000). Nevertheless, we often study the effects of single factors or threats in isolation, or in small combinations. We do this because there are logistical constraints, but also because nature can be complex and unwieldy, and the combined effects of multiple factors operating in combination can mask the effects of single, highly influential factors (e.g., hydrosystem passage-caused delayed mortality in Columbia River Salmon, Budy et al. 2002). However, these synergistic effects can be simultaneously even more influential and challenging to understand at the population level, the unit of focus for conservation, as there can be great variation in the response of individuals to specific threats (e.g., disease), and, we are often interested in projecting status and trend into the future and thus contributing additional uncertainty (Figure 5.1).

Whirling disease was introduced from Europe in the mid 1950's and affects primarily fish in the Salmonidae family (Bartholomew and Reno 2002). The disease is caused by the parasite *Myxobolous cerebralis*, a multiple-host parasite using both fish and aquatic oligochaete worms (*Tubifex tubifex*) as hosts. Like many other emergent infectious diseases (e.g., influenza virus), this parasite has had a wide range of effects on its host (trout) populations ranging from complete and rapid extinction in some streams of Montana and Colorado (Nehring and Walker 1996; Vincent 1996) to undetectable effects on fish survival and abundance (e.g., California; Modin 1998).

The range of effects of disease on trout populations across different areas of North America is likely a result of: 1) differences in susceptibility among different strains, ages, and species of trout (e.g., Vincent 2002; Ryce et al. 2005), 2) the effects of natural, site-specific biotic and abiotic conditions on the establishment, distribution, growth rates, and impacts of the parasite (e.g., Schisler et al. 2000), 3) the effects of

anthropogenic habitat degradation, which are expressed through changes in abiotic conditions and then influence or alter the spread or impact of the parasite (e.g., McWilliams 1999), and 4) the synergistical effects of other threats in combination with disease (e.g., Yellowstone National Park, Stark 2004). Heterogeneity in population-level responses to disease, and the increasing potential for synergistic effects of disease and other threats, make both the prediction of disease impact and the evaluation and implementation of recovery actions extremely challenging.

Bonneville cutthroat trout (*Oncorhynchus clarki utah*) are typical of most endemic trout species throughout the western U.S. in that they were once widely distributed across their range, throughout Utah and in parts of Idaho and Nevada. However, both the distribution and abundance of these fish have declined (USFWS 2001; UDWR 2005) due to the combined effects of habitat degradation and fragmentation, interactions with nonnative species including hybridization, and more recently, disease. The Logan River is part of a large, mountain drainage, located in northern Utah, and home to one of the largest remaining metapopulations of endemic Bonneville cutthroat trout (De la Hoz Franco and Budy 2005). *Myxobolus cerebralis* was first detected in this system in 1999, and since that time, the parasite has spread throughout the drainage and increased in prevalence at most locations. In general, this river drainage remains relatively pristine with an increasing level of anthropogenic impact at lower elevations, and some habitat degradation resulting from grazing in the tributaries. Like many aquatic systems in the west, the Logan River is currently experiencing the effects of an extended, continuous drought with high summer temperatures and low spring discharge (Wilkowske et al. 2003). The drainage is arranged longitudinally from high (2023 m) to low (1352 m) elevation and thus demonstrates a wide range of environmental conditions (De la Hoz Franco and Budy 2005): 1) average summer discharge ranges from 65 cfs (mid-elevation mainstem) to 15 cfs (high elevation tributary), average summer temperature ranges from 9.2 °C (high elevation headwaters) to 12.1 °C (mid-elevation mainstem), and invertebrate densities are typically greater than 2,500 organisms/m². The Logan River is also home to exotic brown trout (*Salmo trutta*), which have likely been present in this system as well as across many streams in the western U.S. and elsewhere, since the late 1800's. Brown trout and cutthroat trout in the Logan demonstrate a distinct allopatric pattern of distribution with cutthroat trout present in high abundance at high elevation sites, brown trout present in high abundance at low elevation sites, and a low combined abundance of both species in mid-elevation, mainstem transition sites (De la Hoz Franco and Budy 2005).

To date, there have been few attempts to synthesize the combination of natural variables and anthropogenic threats that determine fish survival within a framework

for evaluating and predicting the effects of disease at the population level. Here, we use the Logan River metapopulation of endemic cutthroat trout to evaluate the potentially synergistic effects of disease, natural and anthropogenically-altered environmental conditions, and an exotic species. We combine four years of field monitoring and evaluation, laboratory and field experiments across several magnitudes of scale, and population modeling to synthesize and evaluate these effects and to predict the future status of this population.

METHODS

Fish disease, distribution, abundance, and trend

At the inception of the study in 2001, eight long-term index sites were selected that span the longitudinal gradient of the Logan River including the tributaries and a range of anthropogenic impacts (De la Hoz Franco and Budy 2005). Each year, we sampled a suite of abiotic and biotic variables at each site. In addition, we completed depletion population estimates for trout species at each site, retained a subsample of fish for PCR-based DNA analyses of *M. cerebralis*, and monitored fish health and condition. *Myxobolus cerebralis* prevalence was estimated as the percentage of tested fish with any PCR score greater than weakly positive (Figure 5.2). Population trend was estimated using linear regression of log-transformed annual changes in population growth rate as a function of time step (Morris and Doak 2002). To estimate trend, we used data from our four years of depletion sampling (Figure 5.3). We express trend as λ (8), the annual population growth rate with 95% confidence intervals; $\lambda > 1$ indicates positive population trend, $\lambda = 1$ indicates no change in population growth rate, and $\lambda < 1$ indicates the population is declining.

Experimental evaluation of abiotic effects on disease

As noted above, *Myxobolus cerebralis*, the parasite that causes whirling disease, has demonstrated extremely variable effects on trout populations in different streams across the intermountain west. Further, the parasite has a complex two host (oligochaete worms and fish), two stage life cycle such that different life stages of the parasite can experience differential effects of the same environmental variable (e.g., temperature). We investigated the relationship between a selected group of environmental factors, and the distribution and prevalence of *M. cerebralis* in wild salmonid populations in the Logan River (De la Hoz Franco and Budy 2004). Environmental variables included biotic factors (e.g., nutrient composition) and were chosen *a priori* based on demonstrated links to the physiological and ecological preferences and needs of the parasite. Field surveys of fish populations and habitat

characteristics were conducted at all eight long-term index sites described above, during the summers of 2001 and 2002. We also evaluated the relationship between parasite prevalence and the same set of environmental variables with sentinel cage experiments at a subset (six) of the index sites. Sentinel fish experiments were conducted to evaluate the prevalence of the *M. cerebralis* parasite in fish held at and thus exposed only to the sites of interest. Natural field exposures were completed during the summers of 2001 (three sites) and 2002 (three sites) using cutthroat trout alevins (< 5 weeks post-hatch) obtained from a rearing facility free of *M. cerebralis*. After the exposure, survivors were returned to the laboratory, monitored for clinical signs of whirling disease, and ultimately (90 d post-exposure) euthanized for PCR-based tests for *M. cerebralis*. We used regression analyses to identify the environmental variables that best explained the variation in *M. cerebralis* prevalence in cutthroat trout and brown trout across sites. The selection of variables for model development was based on a best-fit model regression; analysis of covariance among variables selected by best-fit indicated that these variables were independent.

The variation in *M. cerebralis* was best explained by a model including water temperature and discharge; these variables were significant overall and explained a large portion of the variation. For cutthroat trout, the model accounted for 74% of the variability in prevalence observed across sampling sites ($df = 11$, Adjusted $R^2 = 0.74$, $P \leq 0.01$). A similar model explained 83% of the variability in prevalence among brown trout. Despite hypothesized mechanistic links to one or more stages or hosts in the *M. cerebralis* life cycle, we observed no relationship between *M. cerebralis* prevalence and substrate composition, nutrients (TN, TP), periphyton, or oligochaete worms; several variables demonstrated collinearity with other dependent variables and thus were not included. Results from sentinel-cage experiments are described later.

Experimental evaluation of competitive interactions

We evaluated the potential for negative impacts of exotic brown trout on endemic cutthroat trout in two sets of experiments completed in 2003 and 2004, at varying spatial scales. In 2003, we held both species in sympatry and allopatry (three treatments per site, six sites; substitutive design) in 20-m² enclosures, arranged across the longitudinal gradient of the Logan River (McHugh and Budy, *in press*). In 2004, we reared cutthroat trout in allopatry and in sympatry with brown trout (two treatments) in 500-m reach sections of three local streams of the Blacksmith Fork River (Chapter 4, *this report*). In both small- and large-scale experiments, we evaluated the performance of individual cutthroat trout based on instantaneous growth and condition. We evaluated growth ($G = [(\ln W_{\text{final}} - \ln W_{\text{initial}}) \cdot t^{-1}] \cdot 100$, where W is

the mass in grams and t is trial length in days). For our large-scale experiment, G was computed for all individual fish in and then summarized across fish within treatment replicates based on the median value. Due to high levels of tag loss in our small-scale study, however, we could not compute growth for all individuals. In this situation, we evaluated growth based on the change in cage-level median weight during the trial period. For both sets of experiments, condition was computed as W_r , (% relative weight) = $W/W_s \cdot 100$, where W is the observed weight of a given fish at the end of the trial, and W_s is its predicted weight (g) based on its measured total length (mm) and a 'standard' length-weight relationship for the species. Our standard length-weight relationship was based on wild cutthroat trout sampled during annual monitoring activities in the Logan River (cutthroat trout $W_s = 6.193 \cdot 10^{-5} TL^{2.670}$; Budy et al. 2004).

In both small (20 m²) enclosures and large (500 m), reach-scale experiments, brown trout clearly reduced the performance of endemic cutthroat trout (Chapters 3 and 4, *this report*). In smaller scale experiments (2003), growth of cutthroat trout was 51% lower when cutthroat trout were reared in the presence of brown trout, as compared to when they were reared only in the presence of other cutthroat trout (McHugh and Budy, *in press*). Similarly, in larger scale experiments (2004), growth of cutthroat trout was 38% lower in sympatric treatments (Chapters 3 and 4, *this report*). Comparisons of diet overlap among natural subpopulations of cutthroat trout and brown trout in allopatry and in sympatry also suggest strong potential for competition. Diet overlap between adult cutthroat trout and both adult and juvenile brown trout was very high in sympatric Logan River populations, and niche width of cutthroat trout broadened greatly from allopatry to sympatry (Chapter 2, *this report*).

Population and simulation modeling of synergistic effects

We built a simple stage-based matrix model to evaluate the combined effects of decreasing population growth rates, increasing disease prevalence, environmental variables including drought, and biotic interactions between endemic cutthroat trout and exotic brown trout. We modeled three of our long-term index sites with sites chosen to represent the range of biotic and abiotic conditions experienced by cutthroat trout across the longitudinal gradient of the Logan River drainage. These sites included (Table 5.1): 1) an allopatric, tributary site occupied solely by cutthroat trout in relatively high abundance (Franklin Basin), 2) a sympatric, mid-elevation mainstem site occupied in near-equal but low abundance by both cutthroat and brown trout (Twin Bridges), and 3) an allopatric, low-elevation mainstem site where both species occur, but brown trout dominate and are very abundant (Third Dam).

Table 5.1. Characteristics of modeled index sites on the Logan River.

| Site | Elevation | Average base-flow discharge ¹ (cfs) | Average summer temperature ¹ (°C) | Percent infected ² | Abundance (fish/km) | |
|----------------|-----------|---|---|----------------------------------|---------------------|----------------|
| | | | | | Cutthroat trout | Brown trout |
| Franklin Basin | 2023 | 13 | 9.2 | 18 | 542 - 1695 | NA |
| Twin Bridges | 1691 | 61 | 11.8 | 89 | 158 - 341 | 338 - 513 |
| Third Dam | 1509 | 38 | 12.1 | 91 | 48 - 75 | 1394 - 2213 |

1. Data from 2001-2002.

2. Average percentage of cutthroat trout infected with *M. cerebralis*, 2003,

3. Range of mean abundance estimates, 2001-2004.

Table 5.2. Model parameter codes, values, and sources used in the matrix model. There are four stages based on length at age estimates from scale data for Logan River cutthroat trout: *Stage*₁₀ = 0-120 mm, *Stage*₂₁ = 121-210 mm, *Stage*₃₂ = 211-290 mm, and *Stage*₃₃ ≥ 290 mm. Each stage has an associated survival rate (*S*) and transition probability (*T*), and adult life stages have fecundity (*F*) values.

| Model Parameter | Base value | Explanation and source |
|------------------------|---------------|---|
| <i>F</i> ₃₂ | 7 | Yellowstone cutthroat trout (YCT) length-fecundity relationship (Meyer et al. 2003), Logan River Bonneville cutthroat trout (BCT) sex ratio information (Fleener 1952), and Westlope cutthroat trout average egg-to-fry survival (Weaver and Fraley 1993) |
| <i>F</i> ₃₃ | 13 | YCT length-fecundity relationship (Meyer et al. 2003), BCT sex ratio information (Fleener 1952), and West-slope cutthroat trout average egg-to-fry survival (Weaver and Fraley 1993) |
| <i>S</i> ₁₀ | 0.01-.13 | Site specific, this study. Value results from calibration to observed trend at site. |
| <i>S</i> ₂₁ | 0.419 | This study, mark-recapture BCT survival estimates, 2002-2003 * |
| <i>S</i> ₃₂ | 0.35 | This study, mark-recapture BCT survival estimates 2002-2003* |
| <i>S</i> ₃₃ | 0.35 | This study, mark-recapture BCT survival estimates 2002-2003* |
| <i>T</i> ₁₀ | 1.0 | Hildebrand 2003, BCT |
| <i>T</i> ₂₁ | 0.5 | Hildebrand 2003, BCT * |
| <i>T</i> ₃₂ | 0.5 | Hildebrand 2003, BCT * |
| <i>T</i> ₃₃ | 1.0 | Hildebrand 2003, BCT |

*To be updated with 2004 Logan River cutthroat trout data (Budy and Thiede, *in preparation*)

Model structure, matrix parameters, and literature sources for borrowed values are summarized in Table 5.2. Site specific population growth rates (λ) estimated from observed population abundance data (see above) were adjusted for generation time and then used to calibrate each site-specific, stage-based matrix models. For each scenario, a λ_{base} was first estimated (stable age distribution) by calibrating each site-specific matrix model to the observed population growth rates at each site (Figure 5.3); unaccounted mortality was absorbed by the S_1 survival stage, as this is the parameter for which we have the greatest uncertainty in terms of empirical estimates of survival from the field. Further, site-specific differences in the prevalence of *M. cerebralis* should be expressed at the S_1 life stage, when fry are still small and susceptible (Ryce et al. 2005).

Table 5.3. Scenarios used to model population trends for cutthroat trout at three index sites on the Logan River. An "X" indicates that a certain scenario was modeled.

| Scenario | Franklin Basin | Twin Bridges | Third Dam |
|--|----------------|----------------|----------------|
| Competition arrives | X | <i>b</i> | <i>b</i> |
| Competition reduced | <i>a</i> | X | X |
| Temperature increases | X | X | X |
| Whirling disease increases | X | X ^c | X ^c |
| Competition arrives, Temperature increases | X | X ^b | X ^b |
| Competition reduced, Temperature increases | X ^a | X | X |
| Competition arrives, Temperature increases, Whirling disease increases | X | X | X |

a. Competition (from brown trout) currently does not occur at this site.

b. Competition is already occurring at this site.

c. Whirling disease prevalence is currently near 100% at this site.

The relationship between temperature and disease prevalence was then used to model the effects of continued drought or habitat changes (% prevalence of *M. cerebralis* = $-1.780 + (0.182 \times [\text{average temperature}]) + (0.041 \times [\text{average discharge}]) + (0.001 \times [\text{average discharge}^2])$); Figure 5.4 and De la Hoz Franco and Budy 2004). Similarly, we used the growth results from the competition experiments (Figure 5.5; McHugh and Budy; *in press*) to modify transition probabilities (\sim growth) for cutthroat trout that occupy allopatric and sympatric sites accordingly. As such, cutthroat trout which occur in sympatry with brown trout were modeled with a transition probability 45% (the average reduction in growth observed across the two experiments) less than the rate of cutthroat trout which occur in allopatry. These modeling scenarios of potential future abiotic and biotic effects were then evaluated independently, and in combination, for the three sites (Table 5.3). Differences among model scenarios were evaluated and are expressed as relative changes (%) to δ_{base} .

RESULTS

Cutthroat trout are present at six of the eight long-term index sites with greatest abundance observed in mainstem, mid-elevation sites and lower abundance at lower elevation sites where cutthroat trout co-occur with brown trout (Figure 5.3). Despite the recent widespread distribution of *M. cerebralis* (first detected in 1999), the prevalence of the parasite varies considerably across sites with lowest prevalence of *Mc* observed in tributary sites and highest prevalence in mid-elevation, mainstem sites (Figure 5.2). *Myxobolus cerebralis* prevalence continues to vary across sites in association with variation in temperature and discharge, as demonstrated by De la Hoz Franco and Budy (2004). The lowest prevalence among cutthroat trout is consistently observed in the headwaters, where the average summer temperature remains below 9.5 °C, whereas high prevalence is associated with temperatures above 12 °C. Further, prevalence in brown trout and cutthroat trout increases with discharge, reaching its highest levels at sites where the average base flow ranges between 0.7 and 1.1 m³/s. Subpopulations of cutthroat trout measured at the long-term index sites fluctuated in abundance from 2001-2002, but in 2003, a decline in abundance appeared to be occurring, and by 2004, a measurable and significant decline in abundance had occurred at four of six sites occupied by cutthroat trout (see δ 's in Figure 5.3). In contrast, brown trout abundance has remained relatively stable at most sites. Population growth rates at most sites were variable, however, and consequently, 95% confidence intervals around sub-populations where δ 's <1 include the possibility of stable or increasing population growth rates. We acknowledge the short-time series used to calculate population growth rates; however, we only use these values in a relative sense in further simulation modeling.

Model scenarios for which brown trout either invade a new site (competition arrives) or are removed from an existing site (competition leaves) have large, independent effects on population growth rates (Figure 5.6). The effect of the removal of competitive effects (by the disappearance of brown trout) has a greater single effect on population growth rates as compared to the arrival of competition. This asymmetry is driven by the relationship between stage-specific transition probabilities and survival probabilities. Increased temperature, experienced by fish infected with the *M. cerebralis* parasite, also has large, independent and negative effects on population growth rates across sites. At sites where competition currently exists, the elimination of competitive effects over-compensates for the negative effects of increased temperature, and population growth rates increase over δ_{base} values. The effect of the arrival of competition in combination with increased temperature, and continued increases in the rates of prevalence of *M. cerebralis*, have the largest overall effect on population growth rates. These combined effects are consistent across modeled sites; however, increased prevalence of *M. cerebralis* has the least effect at the mid-elevation, mainstem sites due to existing high prevalence rates. The high-elevation, headwater site (Franklin Basin), demonstrates the greatest effect of these combined threats due to currently lower *M. cerebralis* prevalence rates and lack of competitive effects observed as of yet.

DISCUSSION

In the Logan River drainage, the abundance of endemic Bonneville cutthroat trout appears to be declining at most (67%) of the sites where cutthroat trout occur. Further, the parasite that causes whirling disease, *M. cerebralis*, has increased in distribution and prevalence since it was first detected in 1999. All tested sites but one (87%) currently test positive for the parasite, and prevalence increases at each site at an annual average of ~16% per year. Despite these high rates of prevalence, we have observed few ($\leq 1\%$; Chapter 1, *this report*) clinical signs of disease in field-examined trout and cannot quantify the specific effects of whirling disease alone on survival. However, our field results and population-growth modeling indicate that at observed population growth rates, subpopulations of endemic Bonneville cutthroat trout appear to be doomed at some sites. For example, at current rates of decline, the subpopulation at the Twin Bridges site is predicted to be extinct in 11 years (as demonstrated by the probabilistic mean-time-to-extinction at a quasi-extinction threshold of 10 fish). However, given the short, time series available, confidence intervals around δ overlap 1 indicating we cannot completely rule out either a population increase for those sites (where currently $\delta < 1$) or a population decrease for those sites (where currently $\delta > 1$; Morris and Doak 2002). Nevertheless, as noted

by Caswell (2000), this uncertainty does not negate the results but instead is an important component of the results. For a protected, endemic population like the Logan River cutthroat trout population, the possibility of continued declining population trends in the future may call for more conservative management actions.

Our modeling in combination with our empirical data also demonstrates that for fish with whirling disease, increases in temperature could have a large, negative effect on population growth rates in the future. However, the invasion of brown trout or the elimination of brown trout (site-specific), and their negative competitive effects, has the greatest and most consistent (across sites) effect on future cutthroat trout population growth rates. These results suggest that the effects of whirling disease and competition with exotic brown trout may be synergistic, a combination that has lead to unexpected and rapid extinction of a related population of cutthroat trout in Yellowstone National Park. In that system, Yellowstone cutthroat trout (*O. c. bouvieri*) from Pelican Creek became infected with *M. cerebralis* in the late 1990's (as in the Logan River), but by 2004 the population had gone nearly extinct. Those cutthroat trout must face threats from not only whirling disease but also the effects of predation by exotic lake trout (*Salvelinus namaycush*); biologists there speculate that if the fish had to deal with only whirling disease or lake trout, the population decline may not have been so dramatic. Thus our results collectively indicate that management actions which include efforts to reduce the effects of, or eliminate, exotics may offer the greatest potential for ensuring the long-term persistence of cutthroat trout, even in the face of increased prevalence of *M. cerebralis* and continued drought.

There are several important limitations of our modeling results. First, the role of the natural variability of the environmental cannot be overlooked. The Logan River drainage and surrounding areas are in the sixth year of a drought cycle (see Wilkowske et al. 2003), a natural environmental factor that is likely contributing to the decline in observed population growth rates. Our trend data include only years where drought conditions prevailed; as such our modeling describes population growth rates under warm, dry environmental conditions and does not include variability in fish growth and survival, or disease effects, that may occur during high run-off years. However, in addition to snow melt, the Logan River is spring-fed such that during summer months (when field sampling is completed) mainstem base flows fluctuate little and rarely decline below $0.37 \text{ m}^3 \text{ sec}^{-1}$ (~ 13 cfs; De la Hoz Franco and Budy 2005). In our modeling scenarios, in order to be conservative, we considered only the effects of continued drought and/or increased temperature, in terms of disease effects. Our empirical data demonstrate a tight coupling between increased temperature and the prevalence of *M. cerebralis* (De la Hoz Franco and Budy 2004).

Nevertheless, a shift towards cooler, wetter climate could have positive effects on future population growth rates, making our results overly pessimistic.

While recent environmental conditions may amplify declining trends, our lack of inclusion of possible threshold effects may counteract this amplification. Here we do not consider the effects of thresholds in either population growth rates or in the effects of disease (infection level) on the primary host population. Small populations are known to be highly sensitive to stochastic events and often demonstrate unpredictable behavior when abundance drops below a certain threshold (Morris and Doak 2002). This unpredictability can result from the simple chance of hitting a zero or low abundance in a bad year or string of bad years, or from density-dependent effects (e.g., allee effects; Dennis 1989). Similarly, although the exact threshold is not formally quantified for whirling disease, populations may experience an increasing rate of mortality after the spore concentration (i.e., dose) of the parasite exceeds a certain threshold (Markiw 1992). Neither types of threshold effects are modeled here (rates are implicitly assumed to be constant over time), but both would likely result in even more pessimistic predictions about future population growth rates for this metapopulation (Morris and Doak 2002).

The role of anthropogenic habitat degradation must also be considered in terms of the effects of a disease or the combined effects of multiple threats including disease. Based on our empirical results from previous studies, increased stream temperature appears to be coupled with increased prevalence of *M. cerebralis* (De la Hoz Franco and Budy 2004). This relationship is corroborated by known physiological preferences and optima of the parasite, and similar relationships of increasing parasite prevalence and/or affect have been demonstrated both in the laboratory (Reynoldson 1987; El-Matbouli et al. 1999) and in the field (Nehring and Thompson 2001; Hiner and Moffit 2002). Habitat degradation often involves increases in stream temperature: 1) over-grazing can denude riparian vegetation leading to more sunlight reaching the stream surface, 2) reduced flow from dewatering for agriculture or residential use can increase stream temperatures, as water pools heat up and have a longer residence time for natural warming, and 3) as frequently occurs with reservoirs behind dams, epilimnetic surface water released downstream is warmed through lentic stratification. In each of these cases, we would generally predict higher prevalence of the *M. cerebralis* parasite in response to warmer temperatures, a shift originally caused by an anthropogenic habitat change. This is just one example (e.g., increased temperature) of the response of stream habitat to anthropogenic impact. For infectious diseases in general, there are numerous such examples in the ecological literature where the role of humans in the spread and impact of an infectious disease is clear and substantial (e.g., avian influenza and Asian agriculture,

Walters 2004; Dengue fever and urbanization, Schrag and Wiener 1995).

Given the complex relationships between abiotic variables and fish health, degradation of the tributary streams in a system like the Logan River drainage may have even more severe effects on fish population growth rates, as compared to habitat degradation in the mainstem. For this type of mountain system, the tributaries are likely less resilient to degradation (often in the form of over-grazing or stream crossings), because flows are naturally lower and edge effects are greater, with edges being the areas where degradation is often concentrated. Further, from the biological perspective, the streams may provide important rearing grounds for juvenile fish and a refuge from more highly infected mainstem areas. We have observed similar prevalence rates among free-ranging adults and juveniles in mainstem sites; however, prevalence of the parasite in juveniles was considerably lower at the uppermost tributary site (Franklin Basin) and somewhat less at the other tributary site (Twin Bridges), as compared to adults (De la Hoz Franco 2003). Similarly, juveniles from sentinel-cage fish experiments held at the tributary sites from previous years consistently tested 100% negative. Together, these results suggest that infected adults likely move from the highly-infected mainstem to spawn in less infected tributaries. Thus juvenile fish may rear in these less infected tributary areas until they have grown to a body size where the risk of mortality due to *M. cerebralis* infection (or infection in combination with another factor) is low, before moving out into more dangerous (in regards to infection) mainstem areas (Hubert et al. 2002). Like the effects of exotic brown trout and cutthroat trout described above, the effects of stream degradation and whirling disease may be synergistic. These results emphasize the importance of protecting and restoring habitat in tributary spawning and rearing areas, such that factors which appear to increase *M. cerebralis* prevalence, (e.g., warmer temperatures) via the several different pathways associated with the complex life history of the parasite, are minimized.

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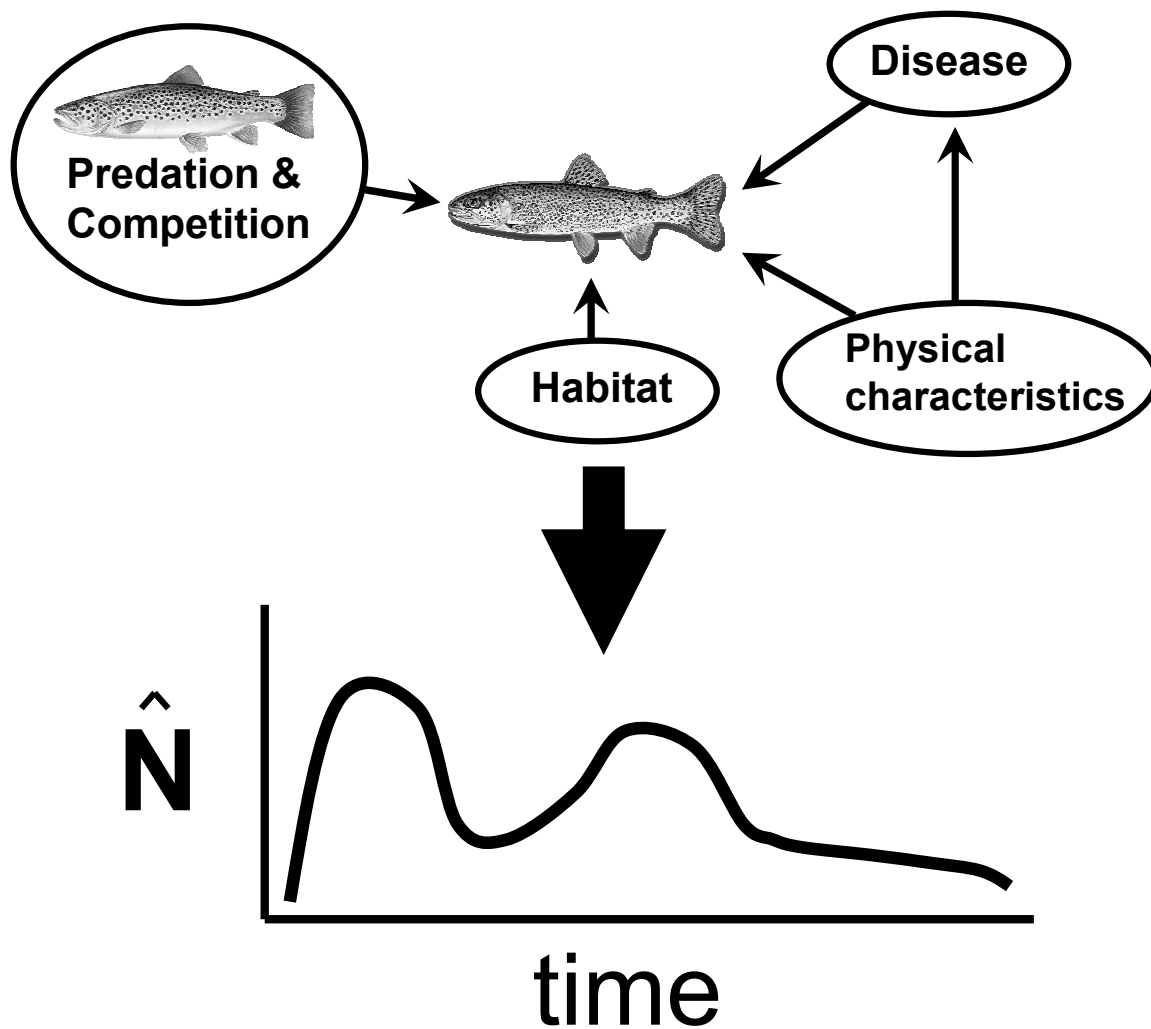


Figure 5.1. Conceptual model of the synergistic effects influencing population abundance of cutthroat trout in the Logan River, Utah.

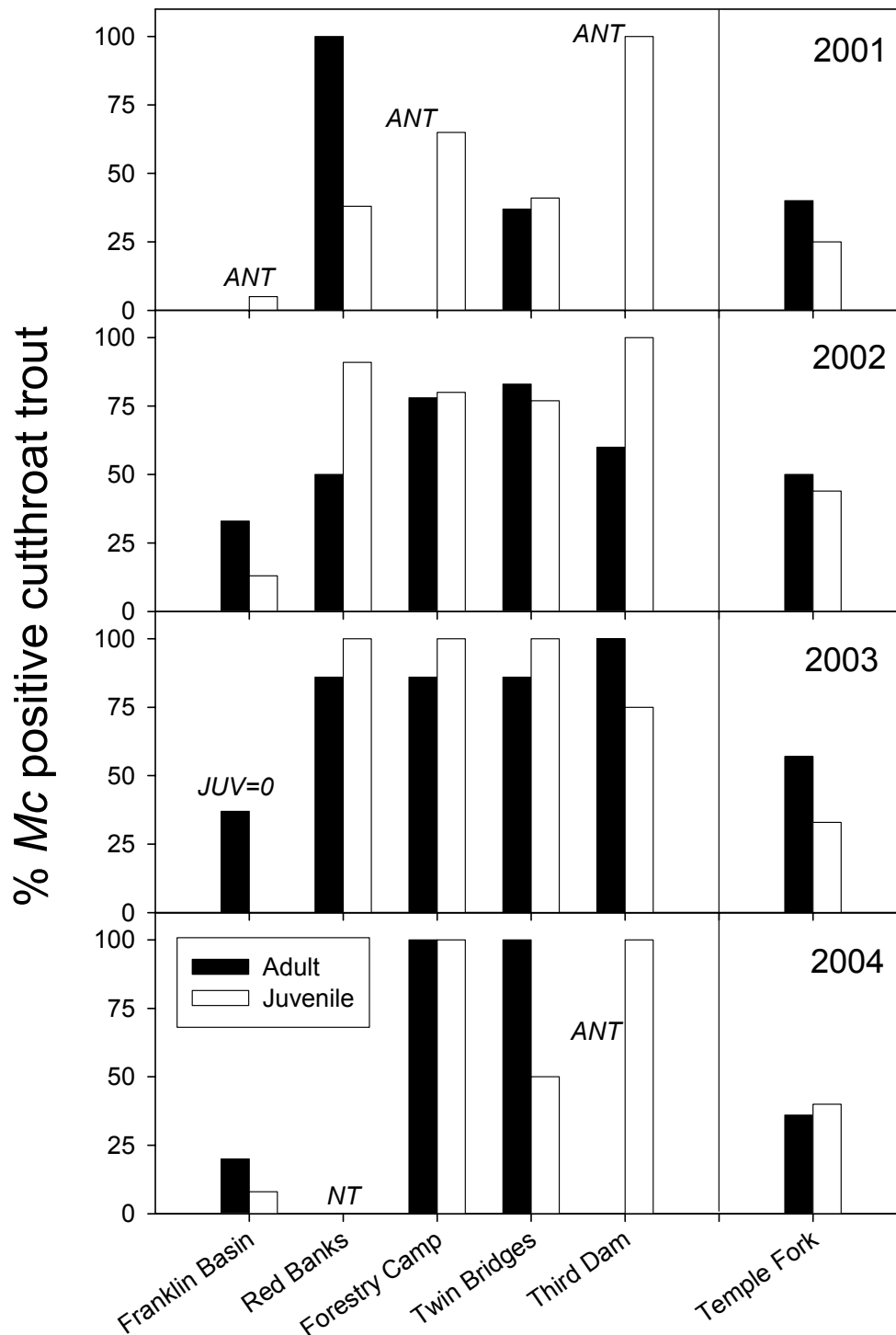


Figure 5.2. Mean percentage of cutthroat trout (all ages combined) by sample site that tested positive for *M. cerebralis* in the Logan River, 2001-2004, based on PCR testing. NS = site not sampled. NC = none captured. NT = samples not tested. ANT = adults not tested.

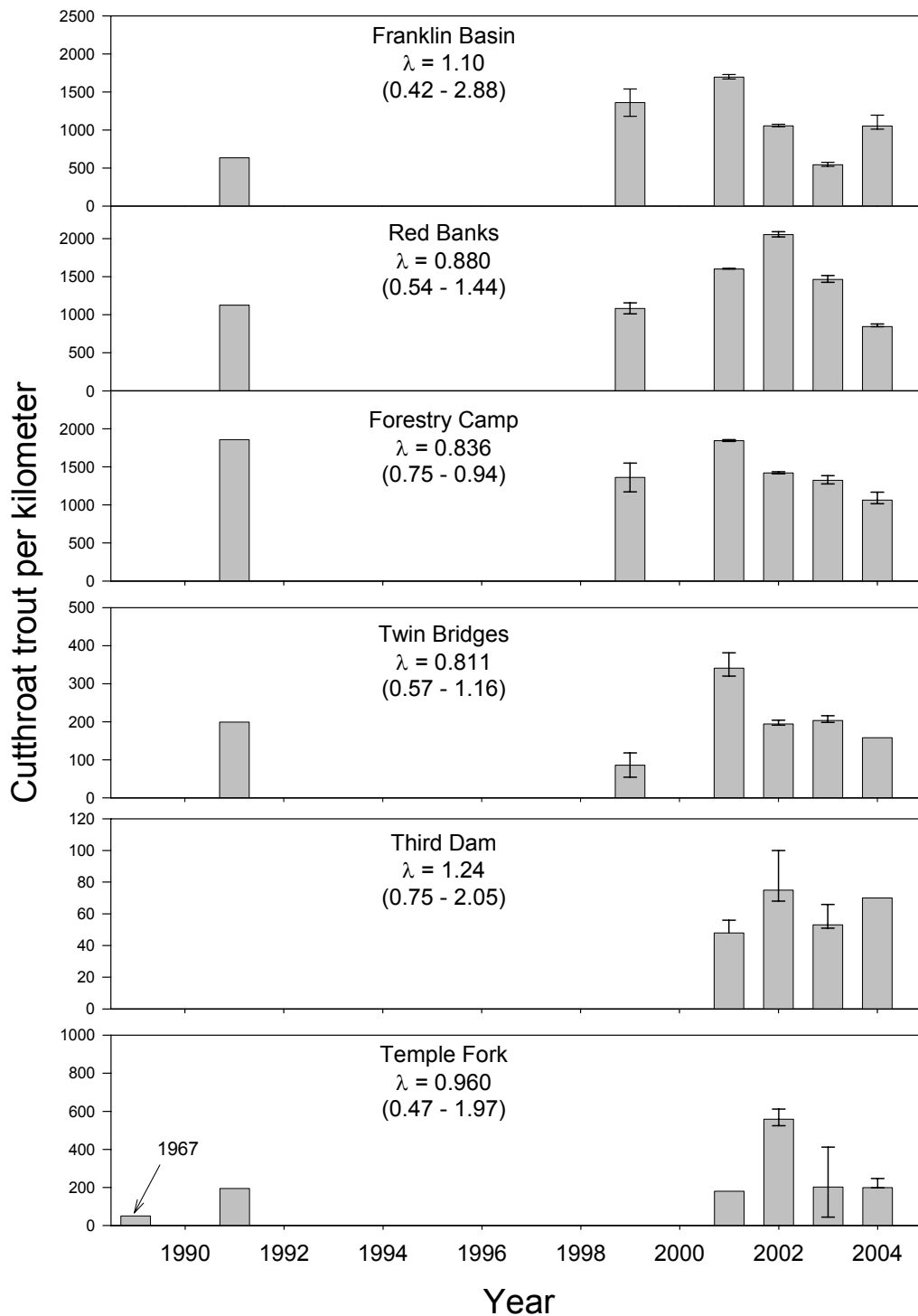


Figure 5.3. Population estimates for cutthroat trout at seven sites on the Logan River, Utah based on the maximum-likelihood removal method in Program MARK (2001-2004 data) and a modified Zippin depletion method (1967-1999 data). Error bars represent 95% confidence intervals (2001-2004) or ± 2 SE (pre-2001 data). Note scale changes in y-axes. Lambda (λ) values with 95% CI are shown for 2001-2004 data.

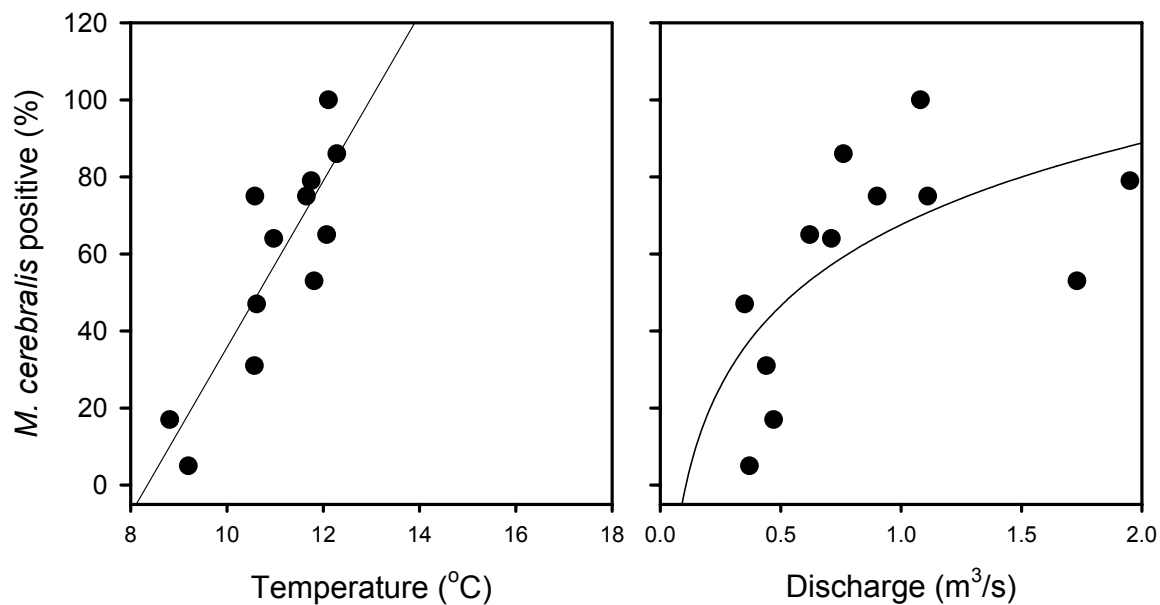


Figure 5.4. Prevalence of infection (% positive for *M. cerebralis*) in cutthroat trout as a function of average summer temperature and discharge in the Logan River, Utah, in 2001 and 2002. A trend line is shown, and a multiple linear regression model including a combination of these two variables was significant ($df = 11$, adjusted $R^2 = 0.74$, $P \leq 0.01$; see De la Hoz Franco and Budy 2004a).

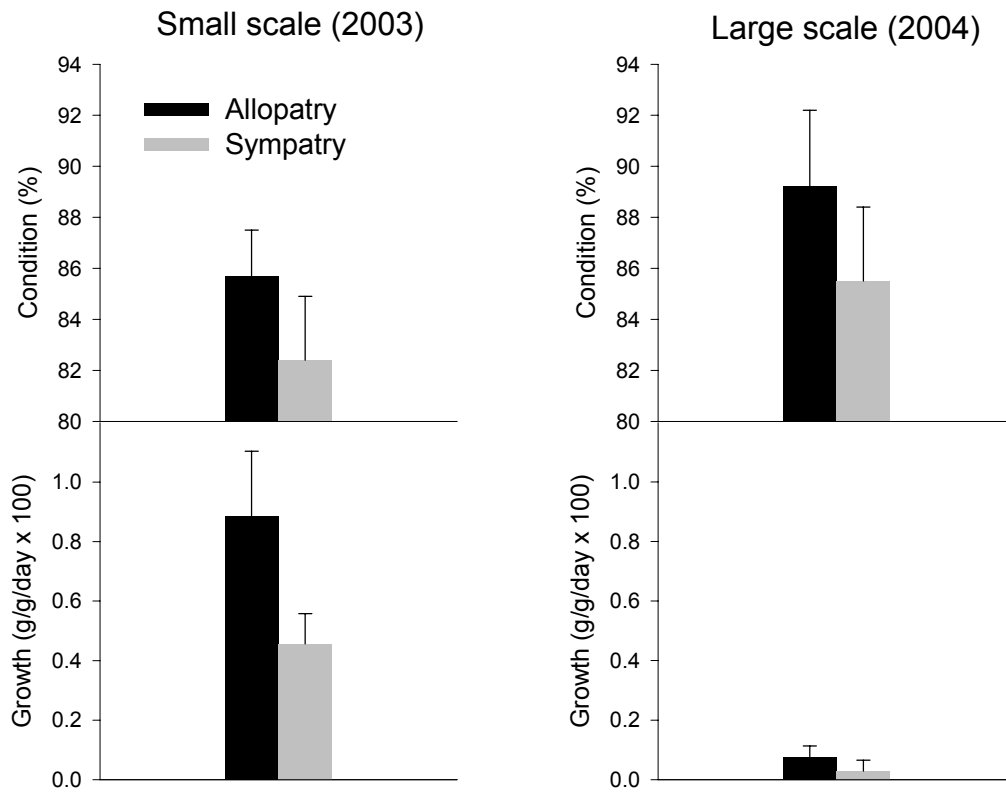


Figure 5.5. Individual-level measures (median growth $\pm 2 SE$ [g/g/day $\times 100$], lower panels; median condition $\pm 2 SE$ [% relative weight], upper panels) of cutthroat trout performance in allopatry (black bars; without brown trout) and sympatry (gray bars; with brown trout). Data are averaged across sites during small-scale (2003) and large-scale (2004) *in situ* experiments (see Chapter 3 and 4, *this report*).

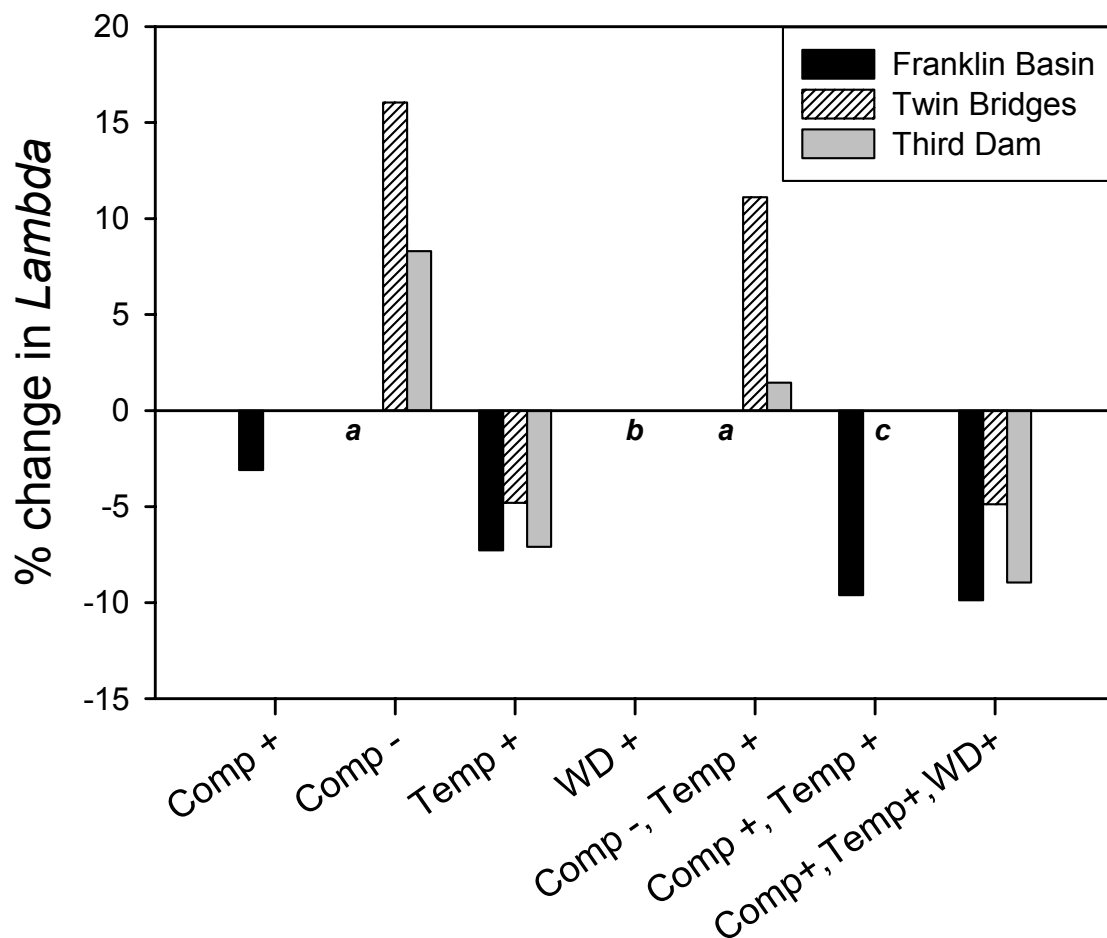


Figure 5.6. Percent change in population growth rate (λ) under different modeling scenarios including arrival (+) or reduction (-) in competition (Comp), increase in prevalence of whirling disease (WD +), and increase in temperature (Temp +). Footnote "a" signifies that this effect comes solely from an increase in temperature as there is currently no competition at this site. Footnote "b" signifies that increases in WD had little effect on λ since the WD parasite currently is in high prevalence at most sites. Footnote "c" signifies that this effect comes solely from an increase in temperature as competition is already present.

APPENDIX

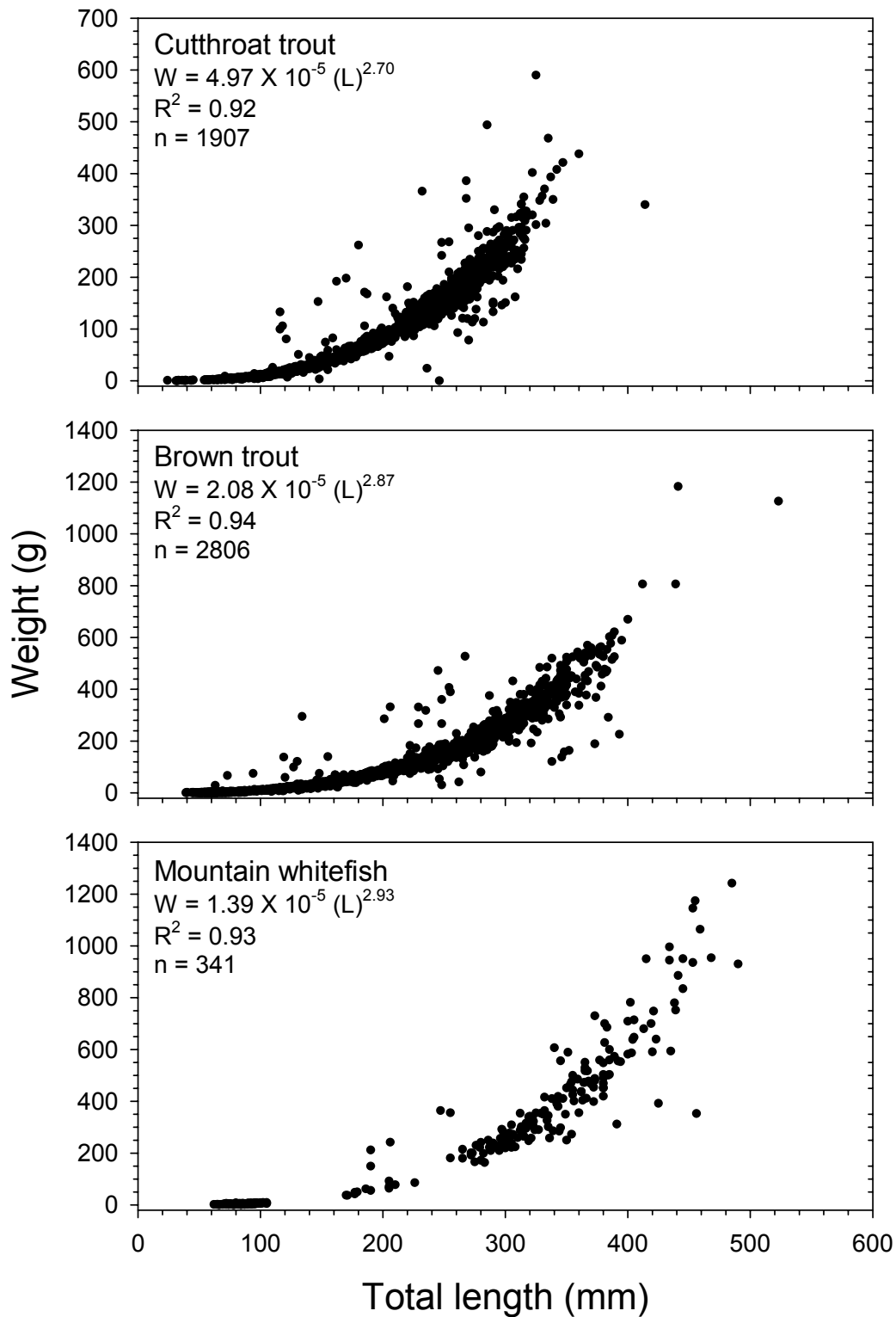


Figure A1. Length-weight regression for cutthroat trout (top panel), brown trout (middle panel), and mountain whitefish (bottom panel) captured in the Logan River, 2001-2004. Regression equations are given along with sample size (n).

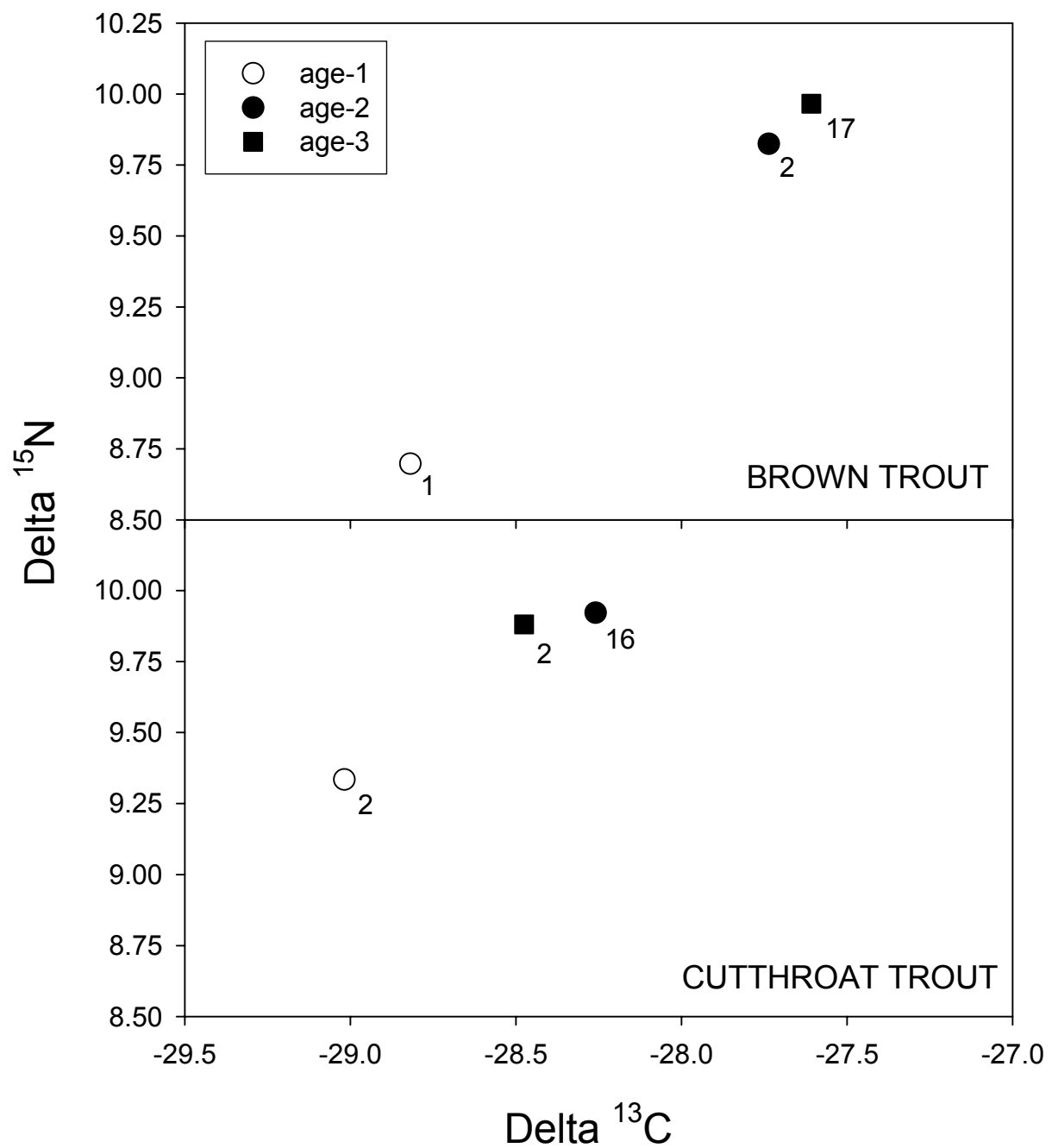


Figure A2. Isotopic-analysis of diets for three age classes of brown trout and cutthroat trout captured in the Logan River, 2004, all sites combined. Sample size is given next to symbols.

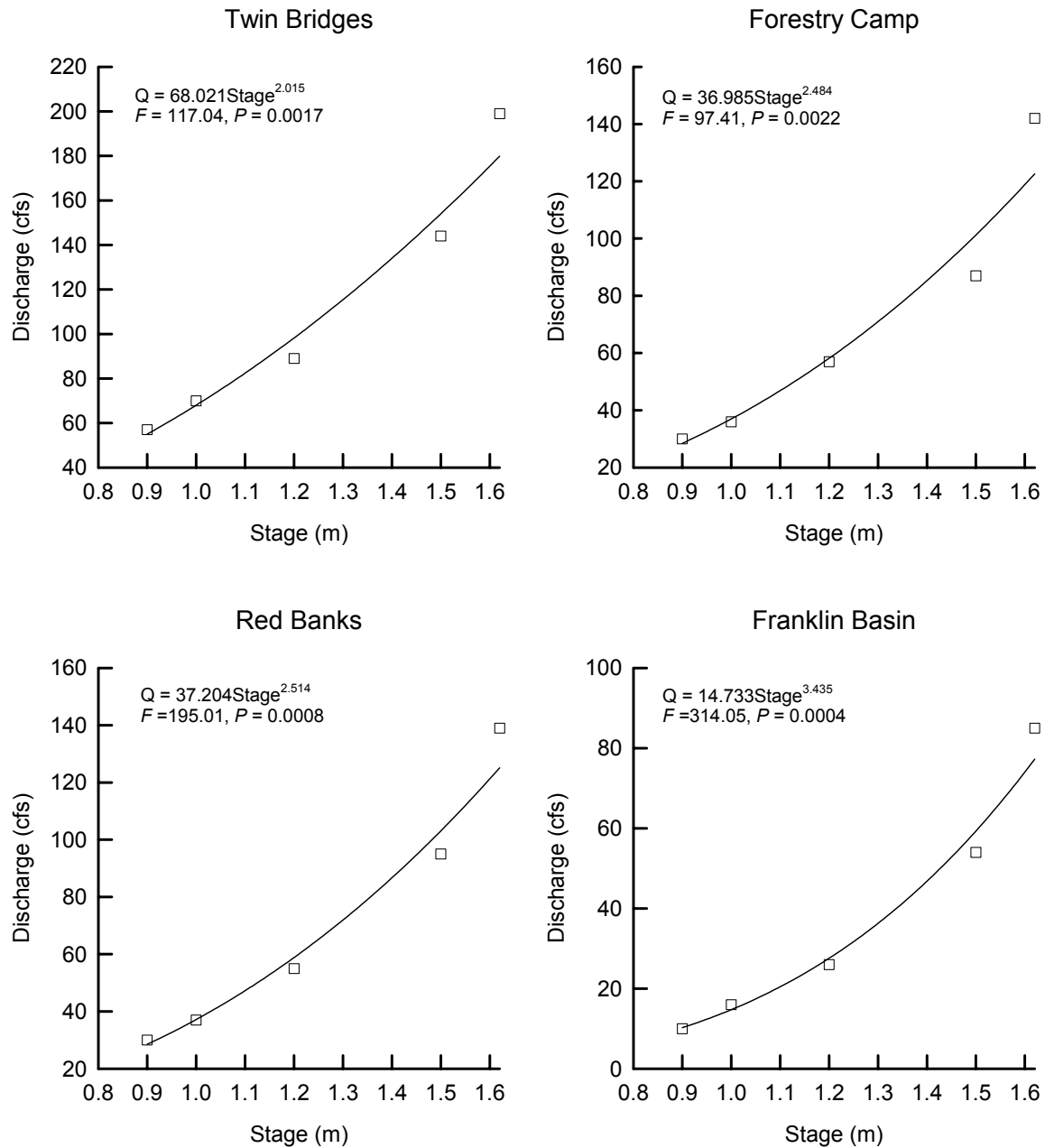


Figure A3. Stage-discharge relationships for the four mainstem sites that are not influenced by irrigation diversions. Regression models explained the variation in flow as a function of water surface elevation at the Franklin Basin bridge well for all sites.

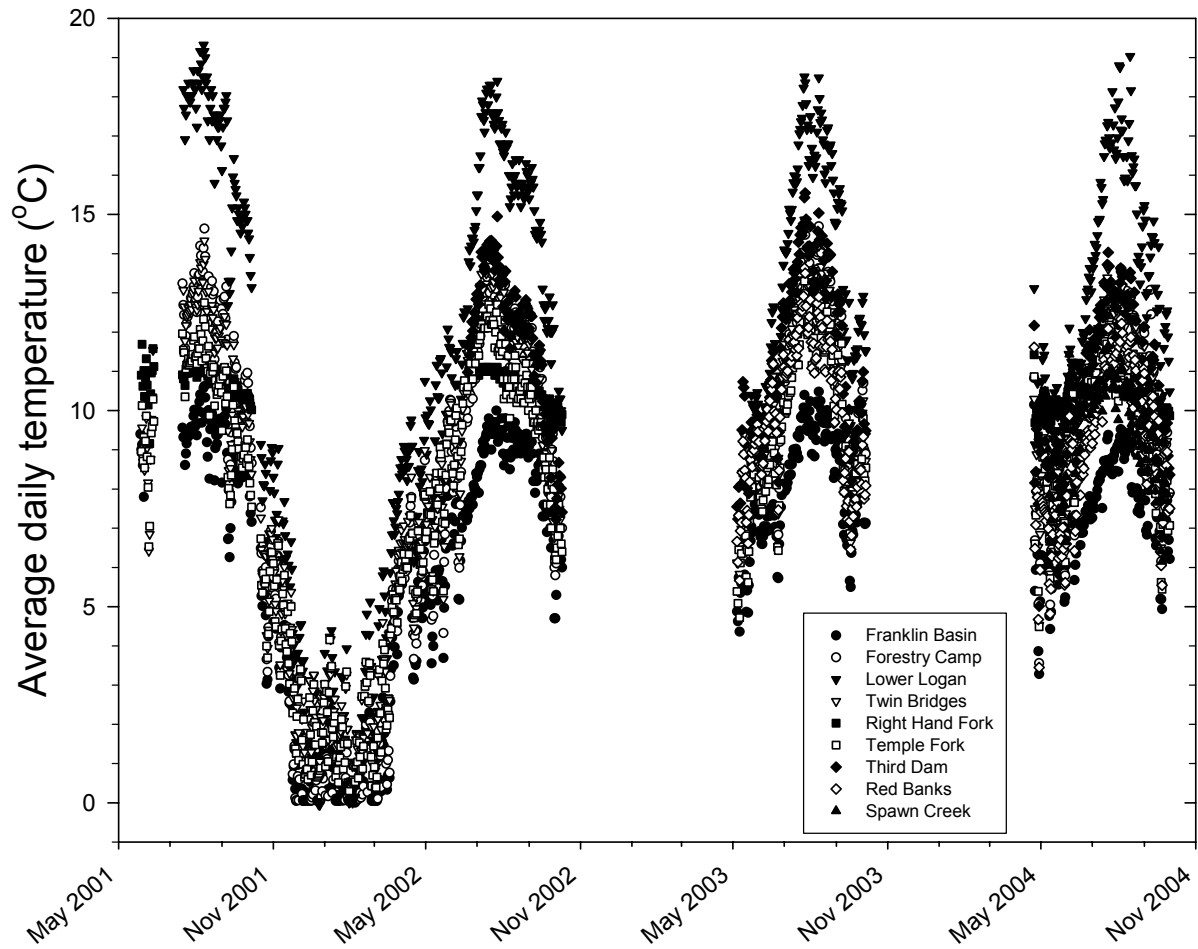


Figure A4. Average daily temperatures at six sites along the Logan River and three tributaries, June 2001 to October 2004.

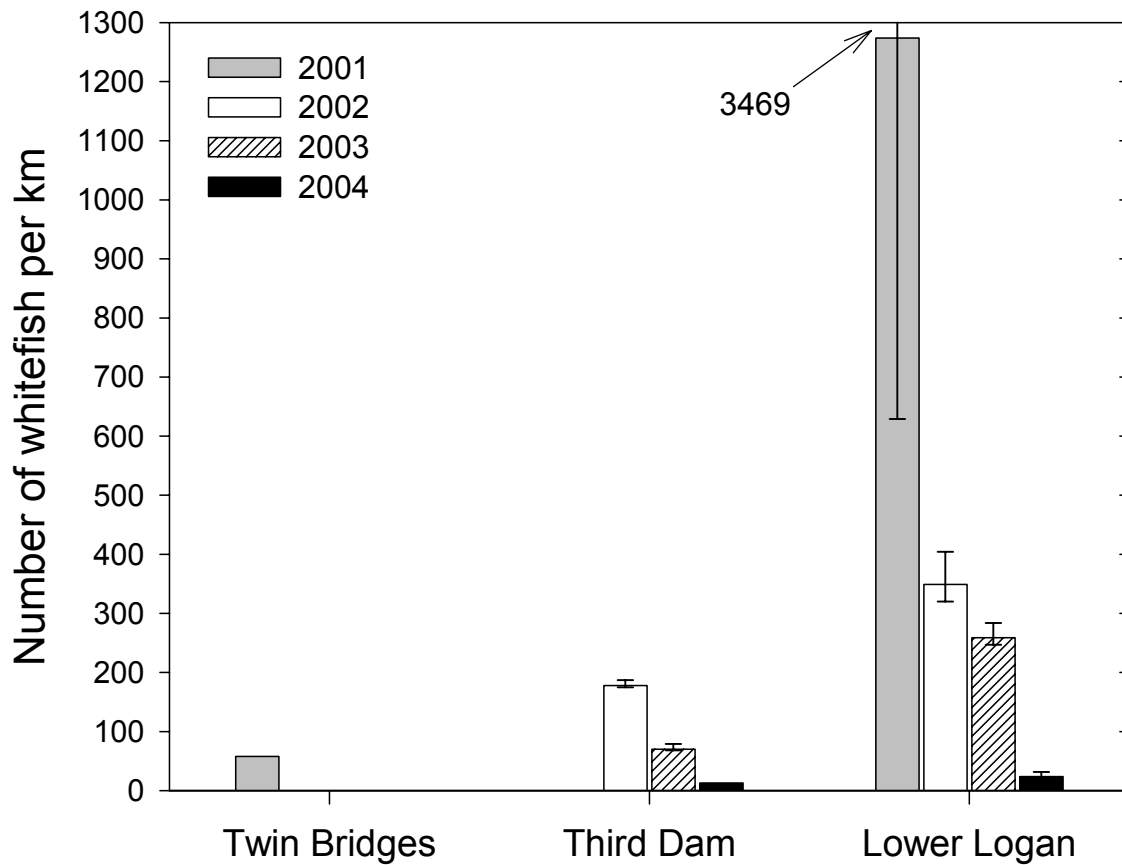


Figure A5. Population estimates (\pm 95% confidence intervals) for mountain whitefish based on the maximum-likelihood depletion estimate in Program MARK, at three long-term index sites on the Logan River where whitefish were captured, 2001 to 2004. Although whitefish were captured at all of these sites since 2001, estimates were not possible during some years due to low capture rates. Number on graph indicates upper 95% CI for the 2001 estimate at Lower Logan.